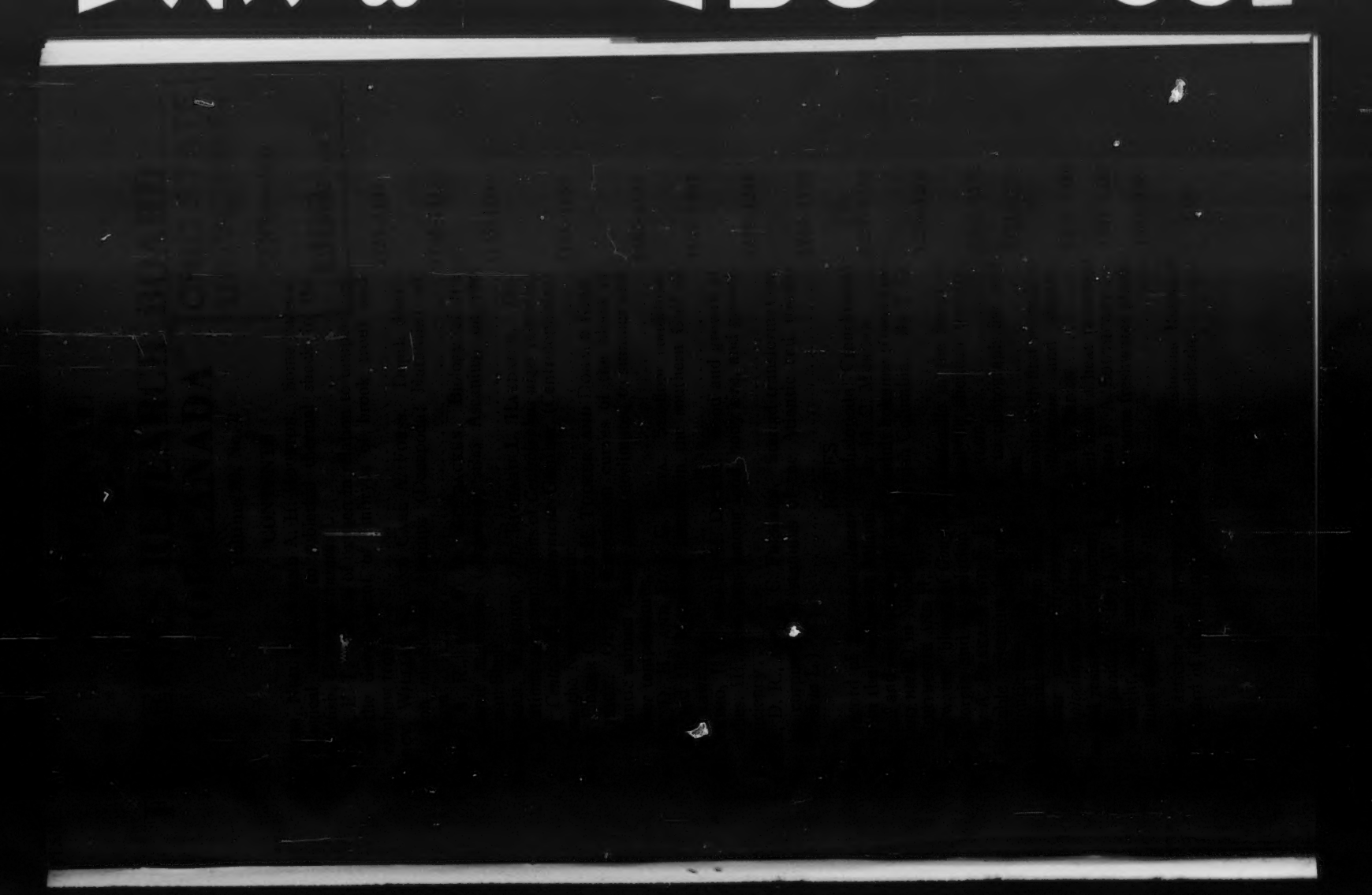

Some Haematological Responses to Sublethal Thermal Shock in the Goldfish, *Carassius auratus* L.[1,2]

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ABSTRACT

Red cell numbers and haematocrit values were notable principally for their constancy during a 10-day experimental period following the exposure of goldfish acclimated to 20 C to an abrupt increase of 10 C in environmental temperature. Mean erythrocytic volume underwent a transient decrease while total blood iron (and presumably haemoglobin) and mean erythrocytic iron content fell slightly during the latter portion of the period of observation. Goldfish maintained at 5 C were typically characterized by two haemoglobin polymorphs, a third fraction being commonly found in animals acclimated at 12, 20, and 30 C. The observations are discussed in relation to the respiratory acclimation of this species to increases in environmental temperature.

INTRODUCTION

Many of the overt consequences of thermal acclimation in poikilothermic vertebrates have been described (Brett, 1956; Fry, 1958, 1964), as have some aspects of the systemic and biochemical adjustments underlying the thermoacclimatory process (Prosser, 1962). In view of the modifications in respiratory metabolism imposed upon these animals by alterations in their thermal environment (Fry, 1957, 1964) some degree of response at the haematological level might, a priori, be expected. This facet of the general problem of thermal acclimation has been investigated in several amphibian (Straub, 1957; Cline and Waldman, 1962; Deb and Boral, 1964) and teleost (Spoor, 1951; Bondar, MS, 1957; Anthony, 1961) species. These studies indicate that haematological variations may in some instances accompany thermal acclimation. However, marked differences have been observed in the haematological responses of quite closely related species (e.g. Straub, 1957; Cline and Waldman, 1962) and, indeed, studies upon the same species have given rise to markedly different descriptions of the thermal response pattern (e.g. Spoor, 1951; Anthony, 1961).

In view of the discrepancies recorded in investigations upon the goldfish, *Carassius auratus*, and as a component of a larger study upon the physiological correlates of the thermal shock response and thermoacclimatory process in

[1]Received for publication January 24, 1966.
[2]Based on a thesis submitted by the senior author in partial fulfilment of the requirements for the degree of Master of Science at the University of Manitoba.
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J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

this species, an investigation of selected haematological parameters was undertaken. While the primary purpose of the study was that of determining what, if any, relationship existed between the haematology and environmental temperature of the animals, it was also hoped that data of this type might be used in the assessment of thermal acclimation rates in the manner outlined in an earlier investigation (Heinicke and Houston, 1965).

The basic protocol of the investigation involved acclimation of the animals to a base temperature of 20 C, followed by their transfer to 30 C. Earlier work upon this species (Fry et al., 1942) had suggested that shifts of greater magnitude might be employed. However, several preliminary trials indicated that transfers from 20 C to temperatures of 35 C or greater proved rapidly lethal to the populations of goldfish available. Consequently, a 20 to 30 C shift was used routinely during the study. Subsequent to transfer, determinations of erythrocyte concentration, haematocrit, and total blood iron were carried out, and values for mean erythrocytic volume and iron content estimated.

In view of the absence of any marked variation in these parameters a preliminary study of possible variations in the incidence and relative abundancy of polymorphic forms of haemoglobin was also undertaken. This aspect of the investigation involved the use of animals acclimated to test temperatures ranging from 5 to 30 C.

MATERIALS AND METHODS

Origin and Maintenance of Experimental Animals

Fish used in the study were obtained from the Goldfish Supply Company, Stouffville, Ontario, in lots of 100–200 animals, and were maintained at the University in continuously aerated and filtered, epoxy resin-coated 80-liter tanks. Water temperatures were controlled to within ± 0.5 C degree of set-point by means of thermistor-activated electronic relays controlling the operation of 500-w resistance heaters. The latter were wrapped with Teflon tape (Johnston Industrial Plastics) to minimize ionic contamination of the tank water.

In view of the known effects of photoperiod upon the thermal responses of this species (Hoar and Robertson, 1959) each tank was hooded, and illumination provided on a 16-hr light – 8-hr darkness schedule. The animals were fed *ad libitum* daily in the early morning upon a food preparation made up for hatchery use by the Fisheries Branch, Department of Mines and Natural Resources (Manitoba). Under this regime they remained in active, and apparently healthy condition during the course of the investigation.

General Experimental Procedure

All animals were held for a minimum period of 28 days at base acclimation temperature (5, 12, 20, or 30 C) before use. This interval, selected upon the basis of earlier studies upon this species (Brett, 1946; Anthony, 1961; Heinicke and Houston, 1965), and as a result of preliminary daily haematological sampling, appeared to be sufficient to ensure completion of the acclimatory process.

Thermal shock was induced by the direct transfer of fish from 20 C to 30 C. The animals were shifted in water with a minimum of handling as it has been well established that a generalized traumatic state is readily induced in teleosts by handling procedures and air exposure. Following transfer the fish were sampled in groups of three, at 12-hr intervals for an initial 96-hr period. Thereafter, samples were taken at 24-hr intervals for a total of 10 days. The values reported for this aspect of the study represent averages obtained from three such trials.

The preliminary investigation upon changes in the nature and occurrence of polymorphic forms of haemoglobin was carried out upon groups of 20 animals acclimated for the time-period previously noted at 5, 12, 20, and 30 C.

Sampling

Individual animals were anesthetized before sampling in aqueous tricaine methanesulphonate (M.S. 222-Sandoz, 300 mg/litre). Blood samples were obtained by bleeding caudally-transected fishes into small polyethylene dishes lightly dusted with dry disodium ethylenediaminetetraacetate to prevent coagulation. Heparin, used by Hesser (1960) and Anthony (1961), and oxalate, used by Field et al. (1943) were found to be unsatisfactory in fully preventing coagulation. Subsamples to be used in determinations of erythrocyte number, haematocrit, and total blood iron were prepared immediately. Samples required for haemoglobin studies were centrifuged for 4 min at 10,000 rpm, the plasma pipetted off, and the packed cells frozen for subsequent analysis.

Haematological Procedures

Erythrocyte counts were carried out according to the procedure described by Hesser (1960), using the diluting solution recommended by Hendricks (1952). The Strumia micromethod was employed in haematocrit determinations, the haematocrit capillaries being sealed with plastic putty (Critoseal) and centrifuged at 7000 rpm for 10 min.

Inasmuch as some controversy still surrounds the reliability of haemoglobin determinations carried out upon fish blood by the usual methods employed in mammalian studies (Anthony, 1961; Larsen and Snieszko, 1961) total blood iron was accepted as an estimate of haemoglobin concentration. The micromethod of Wong as modified by Natelson (1961) was employed with 20-μliter samples of whole blood previously digested in a sulphuric acid-hydrogen peroxide medium.

Values for erythrocyte number (millions/cubic millimeter), haematocrit (per cent), and total blood iron (milligrams per 100 g) were used in the estimation of mean erythrocytic volume, and mean erythrocytic iron content:

1) Mean erythrocytic volume (MEV) = (haematocrit) (10) / erythrocyte number

2) Mean erythrocytic iron content (MEIC) = blood iron / (erythrocyte number/100 ml).

Electrophoretic Separations of Haemoglobin Polymorphs

Separations of haemoglobin polymorphs were carried out by a modification of a method developed for use with goldfish blood (Houston and Falkner, 1963). Frozen samples of packed cells were thawed, suspended in isotonic saline, and washed three times. Following resuspension in distilled water haemolysis was completed by repeated freezing and thawing. As noted previously (Becker et al., 1958; Houston and Falkner, 1963) the resulting haemolyzates were a dark, opalescent brown in colour after centrifugation in contrast to the clear, red-brown solutions usually obtained by similar treatment of human and other mammalian blood samples.

Separations were carried out over 4-hr periods in a Spinco Model R electrophoresis system using Whatman ecteola cellulose, a weakly basic tertiary amine exchanger, as the supporting medium in conjunction with freshly prepared Tris-EDTA-borate buffer (pH 8.9). More consistent and clearly defined fractions were obtained by separation under conditions of constant voltage (500 v) as opposed to constant current (20 ma) as originally recommended (Houston and Falkner, 1963). Following completion of electrophoresis the strips were immediately dried, and scanned at 695 mμ using a Photovolt Model 425 densitometer-recorder assembly.

RESULTS

Haematological Parameters

The mean erythrocyte level observed in goldfish acclimated to 20 C was $2.12 \pm 0.02 \times 10^6$ cells/mm^3 (Fig. 1). Some variation followed the abrupt transfer of the animals from this temperature to 30 C, with group means ranging from 1.81 ± 0.32 to $2.35 \pm 0.2 \times 10^6$ cells/mm^3. No significant overall trend was observed, although two sample group values (60 hr, 144 hr) did differ from the 20 C mean ($p = 0.05$). The slope of the line relating erythrocyte number to time of exposure to 30 C was 0.0002.

A similar situation was noted with respect to haematocrit values (Fig. 2). The maximum deviations from the 20 C level of $29.6 \pm 5.9\%$ occurred at the 60-hr ($25.1 \pm 3.8\%$) and 84-hr ($36.1 \pm 7.8\%$) sampling periods. The absence of any significant trend is indicated by the slope of the equation of haematocrit versus the duration of exposure to increased temperature ($b = -0.005$).

The mean blood iron level among fish acclimated to 20 C was 35.7 ± 7.7 mg/100 g (Fig. 3). Assuming goldfish haemoglobin to be of roughly the same molecular weight and iron content as that of the human, this iron level is equivalent to a haemoglobin concentration of 10.5 g/100 g, a value within the range of concentrations reported by Black (1954) and Klawe et al. (1963) for a variety of marine and freshwater teleosts. Exposure to increased temperature was associated with considerable variation in blood iron levels, observed concentrations ranging from 23.2 ± 3.1 mg/100 g at 216 hr to 42.0 ± 4.3 mg/100 g at the 96-hr sampling interval. The data indicate that a

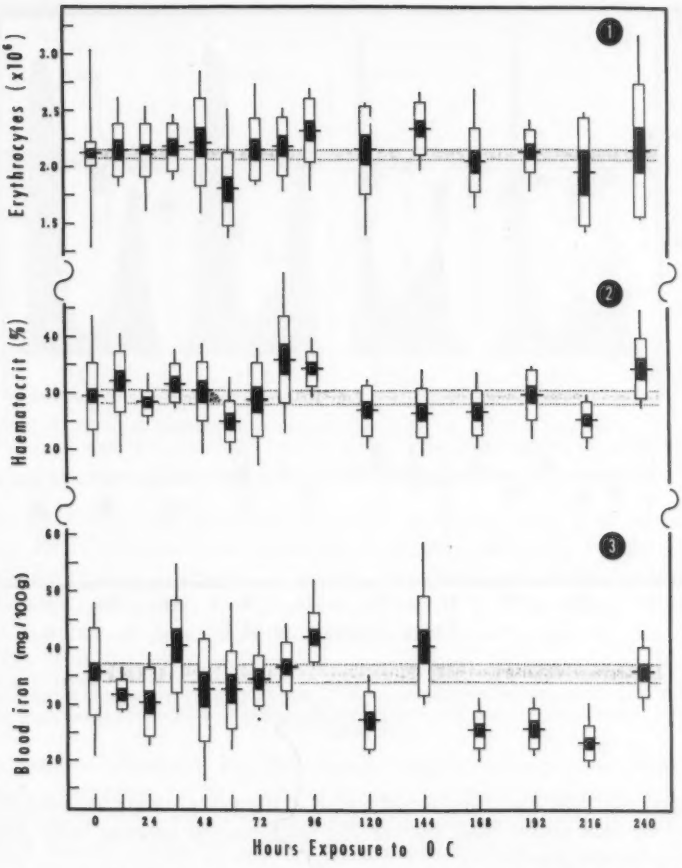

FIG. 1–3. Erythrocyte counts (Fig. 1), haematocrit values (Fig. 2), and blood iron concentrations (Fig. 3) in goldfish acclimated to 20 C, and in animals transferred from 20 to 30 C. Vertical line, range; open vertical bar, one standard deviation; solid vertical bar, one standard error.

slight decrease in blood iron, and presumably haemoglobin level, may have been associated with acclimation to 30 C ($b = -0.027$).

Mean erythrocytic volume (Fig. 4) tended to decrease during the initial period of observation from $163 \pm 30\mu^3$ to a minimum value of $114 \pm 19\mu^3$ (144 hr). Thereafter erythrocyte volume increased, the value in animals acclimated to 30 C for 10 days ($166 \pm 25\mu^3$) being virtually identical to that characteristic of 20 C goldfish.

Mean erythrocytic iron content (Fig. 5) was relatively constant. The minimum and maximum values observed (12.5 ± 1.1, $19.7 \pm 7.0 \times 10^{-11}$ mg/cell) did not differ from that seen at 20 C ($P < 0.05$).

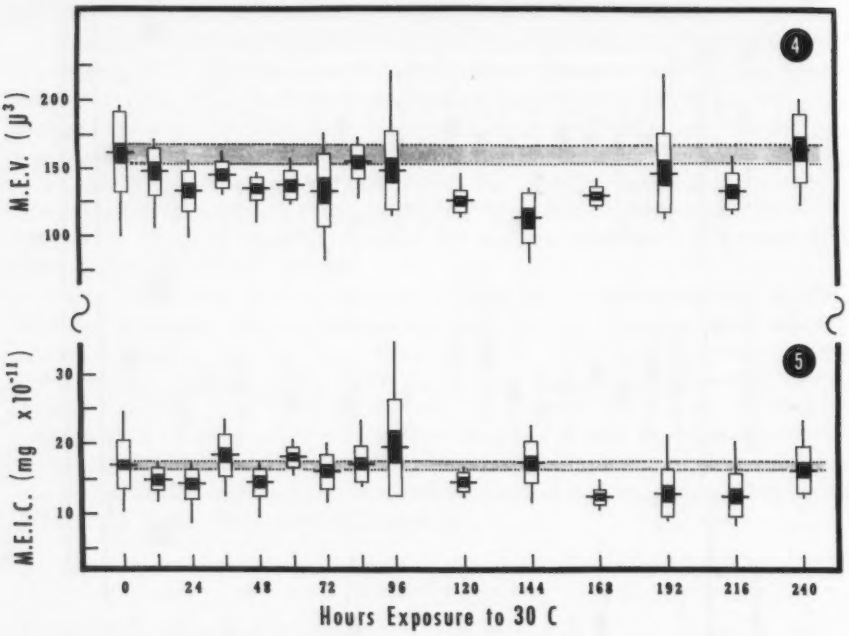

FIG. 4–5. Estimated values for mean erythrocytic volume (Fig. 4) and mean erythrocytic iron content (Fig. 5) in goldfish acclimated to 20 C, and in animals transferred from 20 to 30 C. Vertical line, range; open vertical bar, one standard deviation; solid vertical bar, one standard error

In general, the haematological picture following the temperature shift employed in this study, and during the acclimatory process, was primarily notable for its constancy.

HAEMOGLOBIN POLYMORPHISM

Typical electropherograms obtained for individual fish acclimated to the four test temperatures employed are illustrated in Fig. 6. In each instance the most abundant haemoglobin fraction was a cathodal migrant (C_1) which accounted for from 54.5 ± 8.9 to 64.2 ± 5.4% of total electropherogram density. Among fish acclimated to 12, 20, and 30 C two smaller anodal fractions (A_1, A_2) were normally found. These accounted for from 10.5 ± 2.3 to 16.6 ± 5.6% and from 20.4 ± 8.7 to 31.9 ± 8.9% of the density, respectively. Samples from animals maintained at 5 C, however, usually displayed only a single fraction of anodal mobility, which in this instance constituted 37.2 ± 6.7% of the electropherogram density. The mean electrophoretic mobility of this fraction, 16.0 ± 1.9 mm/4 hr, suggested that it was equivalent to the A_2 fraction (15.0 ± 1.3 mm at 12 C) previously mentioned.

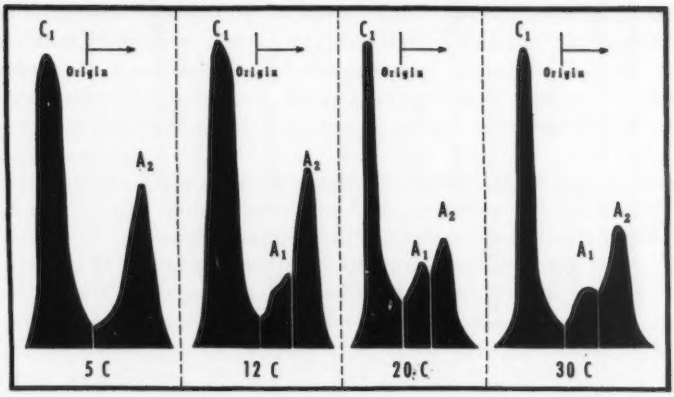

FIG. 6. Typical haemoglobin electropherograms of goldfish acclimated to 5, 12, 20, and 30 C. Ordinate: relative optical density abscissa: relative electrophoretic mobility.

The variability of the data obtained precludes any firm conclusions regarding the significance of thermally induced variations in the concentration of individual fractions. However, the number of fractions evidently increases with acclimation to higher temperatures. It is, perhaps, noteworthy that the number of plasma protein fractions typically seen in this species also varies directly with acclimation temperature (Fenwick and Houston, unpublished data).

DISCUSSION

The values obtained for the haematological parameters investigated in goldfish acclimated to 20 C are, in general, in good agreement with those previously reported for this and other species of freshwater teleosts acclimated to various temperatures (Table I). The most notable discrepancy is seen in the very low value for erythrocyte concentration observed by Baker and Kline (1932). In addition, haematocrit levels, and consequently estimated values for mean erythrocytic volume, are slightly lower than those recorded by Anthony (1961) for this species.

However, the results of the present study are, in certain respects, in distinct disagreement with the findings of some earlier investigations upon haematological responses to changes in the thermal environment. This is particularly true with respect to erythrocyte concentrations. The relatively constant values noted for erythrocyte numbers were consistent with the suggestion that extracellular fluid volume is not greatly modified in the goldfish by thermal changes (Heinicke and Houston, 1965). However, well-defined increases in erythrocyte concentrations have been observed during warm acclimation in the goldfish (Spoor, 1951) and river shiner, *Notropis blennius* (Bondar, MS, 1957), and in the amphibians *Rana esculenta* (Straub, 1957) and *Bufo melanostictus* (Deb and Boral, 1964). Anthony (1961), on the other hand,

TABLE I. Some representative values for haematological parameters in teleost fishes, including variations associated with thermal acclimation.

Species	Acclimation temperature (C)	RBC ($\times 10^6$)	Haematocrit (%)	Blood iron or Hb (*mg/100 g, g/100 g*)	MEV (μ^3)	ME iron or HbC	Reference
Carassius auratus	20	2.12±0.11	29.6±5.9	35.7±7.7 mg/100 g	163±30	17.0±3.5 mg^{-11}	Present study
C. auratus	–	0.5	–	–	–	–	Baker and Kline, 1932
C. auratus	13.9	1.6	–	–	–	–	Spoor, 1951
	30.0	2.2	–	–	–	–	
C. auratus	5, 6	2.0	35.0	10.7[a]	176	53[b]	Anthony, 1961
	26, 30	1.7	34.7	11.1	201	64	
Cyprinus carpio	5 C (approx)	0.84	31.3	10.5 g/100 g	311	72[AA]	Field et al., 1943
Notropis blennius	9.5	1.3	–	3.8 g/100 g	–	–	Bondar, MS, 1957
	16.5	2.7	–	4.9	–	–	
Ictalurus punctatus	–	2.16±0.06	29.4±4.9	6.6±0.3 g/100 g	136[c]	–	Haws and Goodnight, 1962
I. nebulosus	–	1.22±0.04	27.9±6.5	6.9±0.4 g/100 g	228	–	

[a]Reported as whole blood oxygen capacity.
[b]Reported as single cell oxygen capacity.
[c]Calculated from data reported.

reported an inverse relationship between red cell concentration and temperature in the goldfish. Similarly, Haws and Goodnight (1962), in a comparison of the haematological characteristics of the channel catfish, *Ictalurus punctatus*, and brown bullhead, *I. nebulosus*, found that the former species, which normally inhabits colder waters than the bullhead, typically possessed larger numbers of smaller erythrocytes.

More consistent results have been obtained with respect to haematocrit levels. As previously noted there was little evidence indicative of any overall temperature-associated change in haematocrit levels in the goldfish. Anthony (1961) arrived at a similar conclusion following studies upon warm (26, 30 C) – and cold (5, 6 C)–adapted goldfish, while Haws and Godnight (1962) recorded comparable values for haematocrit levels in the channel catfish and brown bullhead. It is perhaps of interest that quite different findings have been reported for amphibians. Thus, while Deb and Boral (1964) found no difference in the haematocrits of toads held at 6 and 32 C, Cline and Waldman (1962) reported an inverse relationship with temperature in *Rana pipiens*, and Straub (1957) observed an increase in haematocrit level at higher temperatures in *R. esculenta*.

Anthony (1961) reported an inverse relationship between mean erythrocytic volume and temperature, a finding generally consistent with the situation described for *I. punctatus* and *I. nebulosus*. The data obtained in the present study suggest that a transient decrease in cell volume followed transfer to 30 C. It is perhaps noteworthy that Anthony employed acclimation times of as little as 1 week, and that it was between 6 and 8 days after transfer that minimum values for this parameter were observed in the present study.

Total haemoglobin levels do not appear to be markedly influenced by the thermoacclimatory process. The single exception to this generalization is found in the work of Bondar (MS, 1957), who reported an increase of approximately 50% in the haemoglobin content of the blood of the river shiner following transfer from 9.5 to 16.5 C. However, the levels reported and the analytical techniques employed suggest that the data may be of doubtful validity. On the other hand, Anthony's conclusion that the oxygen-carrying capacity of single erythrocytes increases slightly at higher temperatures is difficult to reconcile with changes in mean erythrocytic iron content. The incidence of a third haemoglobin fraction at temperatures above 12 C may, however, have some bearing on this question.

The observations made in this investigation, when taken in context with earlier studies suggest that, on the whole, adaptive variations at the haematological level are probably not of overriding importance in the process of thermal acclimation in teleosts. While some distinctive trends have been reported in certain species the lack of consistency in the results obtained, especially in separate studies upon the same species held under essentially similar thermal conditions (Spoor, 1951; Anthony, 1961; present study), suggests that the changes observed may not be attributable to temperature *per se*.

They may well represent the influence of uncontrolled intrinsic or extrinsic agencies (e.g. photoperiod, diet, age, level of sexual maturity) working individually or in conjunction with temperature (Haws and Goodnight, 1962.

This hypothesis is, perhaps, unexpected in view of the well-defined relationship between temperature and respiratory metabolism in teleosts. A recent analysis of teleostean respiratory mechanisms and their control (Hughes, 1964) suggests, however, that adaptations to the type of environmental stress imposed in this study and in those previously cited may involve one or several of a variety of sites. Two possibilities may be briefly mentioned in illustration.

Adaptive shifts in the oxygen dissociation curve may be of distinct compensatory value. Such changes have been well documented (Kawamoto, 1929; Irving et al., 1941) in fishes acclimated to different temperatures, and are also found in closely related species occupying distinct thermal environments. The recent studies of Burke (1965) upon oxygen dissociation curves and haemoglobin variants in the bass *Micropterus dolomieui* and *M. salmoides* suggest that changes in haemoglobin types of the sort reported in the present investigation may well be of some importance.

The recent study by Steen and Kruysse (1964) upon patterns of branchial circulation in several teleostean species also suggests a probable mode of adaptative response. These authors have convincingly demonstrated the existence of alternate respiratory and nonrespiratory flow pathways through the gill filament. Thus, a potentiality exists for adaptive modification of effective respiratory surface area. Flow pathways were also found to be sensitive to endocrine action, with adrenaline increasing volume flow through the lamellar regions of excised gills, while acetylcholine treatment tended to cause the diversion of flow through the nonrespiratory central cavities of the filament. These observations are of particular interest in view of the recent studies of Mahon et al. (1962) and Weatherley (1963) on the relationship between environmental temperature and adrenal activity in golfish, and river perch, *Perca fluviatilis*. In both studies heat-shock and warm acclimation were associated with evidence of increased secretory activity. A functional identity between the chromaffin tissue of teleosts and the adrenal medulla of higher vertebrates appears to be likely (Gorbman and Bern, 1962). Thus, respiratory adaptation in teleosts subjected to increased environmental temperature may involve hormonally-induced increases in blood flow through the gill areas associated with gas exchange. In short, the puzzling diversity of haematological responses in teleosts, and their generally low order of magnitude, may represent the reliance of the animals upon adaptive responses other than the presumably more metabolically expensive processes of erythrocyte elaboration and haemoglobin synthesis.

ACKNOWLEDGMENTS

The authors wish to acknowledge the support provided by the Fisheries Research Board of Canada and the National Research Council of Canada for this and related studies.

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Effects of Oxygen in Relation to Temperature on the Development of Embryos of Brook Trout and Rainbow Trout[1]

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ABSTRACT

Embryos of the brook trout (*Salvelinus fontinalis* Mitchill) were incubated in reduced levels of dissolved oxygen of approximately 2.5 ppm, 3.5 ppm, 4.5 ppm, and a control level near air-saturation (10 ppm) at each four temperatures, 2.5, 5.0, 7.5, and 10.0 C, from fertilization to a late stage of development. Embryos of the rainbow trout (*Salmo gairdneri* Richardson) were incubated in a similar experiment at levels of oxygen approximating 2.5 and 3.5 ppm and a level near air-saturation at each of the four temperatures, to a similar, late stage of development. A third small experiment was conducted in which embryos of rainbow trout were incubated at 12.5, 15.0, and 17.5 C, at a level of dissolved oxygen near air-saturation. In all instances for both species the velocity of embryonic development, measured by the times required to attain a series of selected embryonic stages, was accelerated by increasing temperature. The velocity of development was increasingly retarded by progressively lower levels of dissolved oxygen. The times required to affect hatching and the lengths of the periods of hatching were similarly influenced by temperature and by the level of dissolved oxygen. These findings are discussed in the light of pertinent literature.

INTRODUCTION

This report is a presentation of additional information on the influence of two primary environmental variables, temperature and level of dissolved oxygen, on certain aspects of the development of salmonid embryos, from work which was begun in the autumn of 1957. The first paper (Garside, 1959) described the influence of temperatures and various levels of oxygen on the velocity of development, the time of hatching, and the induction of some teratologic conditions in embryos of lake trout (*Salvelinus namaycush* Walbaum). The experiments in this report were similar in procedure to the experiment on lake trout and were performed on embryos of the brook trout (*Salvelinus fontinalis* Mitchill) and the rainbow trout (*Salmo gairdneri* Richardson).

MATERIALS AND METHODS

Approximately 12,000 freshly fertilized brook trout eggs were obtained from the Ontario Department of Lands and Forests hatchery at Mount Pleasant, Ont., on October 26, 1957. The eggs were packed in crushed ice and *Sphagnum*

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J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

in a conventional egg carrier and transported to the Laboratory for Experimental Limnology at Maple, Ont., where they were divided into 16 approximately equal lots and placed into 16 experimental environments for incubation, within 4 hr of fertilization.

The apparatus employed for controlling the temperature of water and the levels of dissolved oxygen and other details of the performance of this experiment have been previously described by Garside (1959). Incubation temperatures of 2.5, 5.0, 7.5, and 10.0 C were employed in this experiment. Separate supplies of water having three reduced levels of dissolved oxygen, approximating 2.5, 3.5, and 4.5 ppm, were employed at each of the four temperatures. The remaining four lots of eggs were supplied with water with levels of dissolved oxygen close to the values for air-saturation at each of the four temperatures. This information is presented in Table I along with the number of days of exposure to low levels of dissolved oxygen for each of the lots being treated. Laboratory tap-water equilibrated to the appropriate temperatures was provided for all lots of eggs when the treatments with low levels of oxygen were terminated. The respective temperatures were maintained to the end of the hatching period for each lot of embryos.

On April 16, 1958, approximately 15,000 freshly fertilized rainbow trout eggs were obtained from the Ontario Department of Lands and Forests hatchery at Normandale, Ont. These eggs were transported to the Maple Laboratory and apportioned into 11 approximately equal lots. These lots were placed

TABLE I. Experimental environments for incubation of brook trout eggs in the 1957 experiment. Treatments of embryos with the three lower levels of dissolved oxygen were terminated and the control levels of oxygen were restored at the times indicated, when the embryos were in an advanced state of development.

Mean temp (*C*)	Mean dissolved oxygen (*ppm*)	Oxygen treatment (*days*)	Mean temp (*C*)	Mean dissolved oxygen (*ppm*)	Oxygen treatment (*days*)
2.5±.1	2.6±.2	77	7.5±.1	2.6±.2	53
2.5±.1	3.7±.2	77	7.5±.1	3.4+.2	53
2.5±.1	4.5±.2	77	7.5±.1	4.3±.1	53
2.5±.1	10.5±.1[a]	–	7.5±.1	10.3±.2[a]	–
5.0±.1	2.6±.2	69	10.0±.1	2.5±.1	45
5.0±.1	3.6±.2	69	10.0±.1	3.3±.2	45
5.0±.1	4.4±.2	69	10.0±.1	4.2±.1	45
5.0±.1	10.4±.2[a]	–	10.0±.2	10.2±.2[a]	–

[a]Control level of dissolved oxygen.

in the incubation apparatus used in the earlier experiment for brook trout eggs. Temperatures and levels of dissolved oxygen were controlled in the same manner.

Four temperatures were also used in this experiment, 2.5, 5.0, 7.5, and 10.0 C but only two reduced levels of dissolved oxygen were used; they approximated 2.5 and 3.5 ppm. At 2.5 C only one reduced level, approximately 2.5 ppm, was used. The control lots were incubated in air-saturated tap-water regulated to the required temperatures. The details, including the duration of treatments, are shown in Table II.

Following the termination of treatments with reduced levels of oxygen each lot of eggs was provided with tap-water maintained at the required temperature until all of the embryos had hatched.

TABLE II. Experimental environments for incubation of rainbow trout eggs in the 1958 experiment. Treatments of embryos with lower levels of dissolved oxygen were terminated and the control levels of oxygen were restored at the times indicated, when the embryos were in an advanced state of development.

Mean temp (*C*)	Mean dissolved oxygen (*ppm*)	Oxygen treatment (*days*)	Mean temp (*C*)	Mean dissolved oxygen (*ppm*)	Oxygen treatment (*days*)
2.5±.1	2.9±.3	80	7.5±.1	2.6±.2	45
			7.5±.1	3.7±.2	45
2.5±.1	11.3±.1[a]	–	7 5±.1	10.6±.2	–
5.0±.1	2.8±.2	65	10.0±.1	2.5±.2	34
5.0±.1	3.9±.1	65	10.0±.1	3.5±.2	34
5.0±.1	11.3±.1[a]	–	10.0±.1	10.5±.1[a]	–

[a]Control level of dissolved oxygen.

In the spring of 1959 an additional experiment was performed to obtain information concerning the development of rainbow trout embryos incubated at temperatures higher than 10 C. On April 23, about 3500 eggs were taken from a large rainbow trout caught in the Nottawasaga River near Alliston, Ont. These eggs were fertilized with sperm from a male rainbow trout also captured there. The eggs were divided into three lots and placed in hatchery baskets suspended in troughs of running, aerated tap-water heated to 12.5, 15.0, and 17.5 C, at the Maple Laboratory within 2 hr of fertilization. These temperatures were maintained until after all of the embryos had hatched in each lot.

In the three experiments just described the progress of development of the embryos was followed by observation of samples of five eggs which

were collected at regular intervals and preserved in Davidson's solution. Brook trout eggs and rainbow trout eggs incubated at 2.5 and at 5 C were sampled at the end of day number one and at the end of every alternate day thereafter. Sampling was begun at 2 PM. Eggs incubated at 7.5 C and at 10 C were sampled daily beginning at 2 PM. Rainbow trout eggs in the third experiment were sampled 8 hr after fertilization, at 8 PM, and every 12 hr thereafter.

Eighteen developmental stages listed by Garside (1959) were used to follow the development of the various lots of embryos. The embryos of a sample were considered to have arrived at a specific stage when at least three of the five embryos exhibited the features of that stage. Four of the stages, 4, 8, 12, and 16 are employed for special consideration in Results section and the descriptions of these are repeated in Table III.

With the onset of hatching the number of embryos which hatched each day in each lot was recorded and the median hatching times were determined. The number of days of incubation prior to the beginning of hatching plus the number of days taken to reach the median hatching day in the hatching period were considered to constitute the *period of incubation*.

TABLE III. Four selected embryonal stages of development in salmonid fishes. Numbers of the stages are those employed in an expanded series (Garside, 1959).

No.	Stage	Description
4	One-quarter epiboly	Germ ring has overgrown one-fourth of yolk; embryonic shield elongating.
8	Blastopore closed	Lips of blastopore have grown together forming a terminal node on segmenting trunk.
12	One-quarter vitelline venation	Network of vitelline veins is distributed through posterior one-quarter of yolk-sac.
16	Notochord upturned	Posterior portion of notochord flexed caudodorsad.

RESULTS

EFFECTS OF TEMPERATURE ON DEVELOPMENTAL RATE AND HATCHING

BROOK TROUT

The times, in days, required by embryos of the various lots of brook trout to attain each of the 18 designated stages have been listed in Table IV. These figures show the typical relation of the velocity of development to temperature: the time for development decreases with increasing temperature, as shown also in Fig. 1. The time required to pass the 18 stages varied from 94 days at 2.5 C to 34 days at 10 C. There is some curvature in the lines for stages 12 and 16 in Fig. 1. This indicates that the acceleration of the rate of development at these stages through the range of temperature from 2.5 to

TABLE IV. Times, in days, required by the lots of brook trout embryos, incubated at four temperatures and four levels of dissolved oxygen, to reach 18 selected stages of development in the 1957 experiment. Columns are headed by mean levels of dissolved oxygen expressed as parts per million.

	2.5 C					5.0 C				
Stage	2.6	3.7	4.5	10.5		Stage	2.6	3.6	4.4	10.4
1	3	3	3	3		1	3	3	3	3
2	9	9	9	9		2	7	7	7	7
3	17	17	17	15		3	13	13	13	11
4	24	24	24	23		4	17	17	15	15
5	26	26	26	24		5	19	18	17	17
6	28	28	28	27		6	22	21	21	19
7	32	31	31	29		7	24	24	23	21
8	38	34	34	32		8	26	26	25	23
9	42	41	41	39		9	33	32	31	25
10	49	49	49	47		10	36	35	35	32
11	59	55	55	50		11	38	37	37	36
12	61	59	59	57		12	41	39	39	38
13	63	64	63	60		13	45	41	41	40
14	74	71	68	64		14	51	48	48	43
15	78	77	74	67		15	55	51	51	47
16	87	83	80	73		16	63	59	53	51
17	99	95	94	88		17	67	65	64	58
18	105	99	97	94		18	81	78	75	70
	7.5 C					10.0 C				
Stage	2.6	3.4	4.5	10.3		Stage	2.5	3.3	4.2	10.2
1	2	2	2	2		1	2	2	2	2
2	6	6	6	6		2	5	5	5	5
3	9	9	9	9		3	7	7	7	6
4	12	12	12	11		4	9	9	9	8
5	13	13	13	12		5	10	10	10	9
6	15	15	14	13		6	11	11	11	10
7	16	16	16	15		7	12	12	12	11
8	19	19	19	16		8	13	13	13	12
9	22	21	21	20		9	17	17	16	15
10	24	24	23	22		10	19	19	18	17
11	26	25	25	23		11	21	21	20	19
12	28	27	27	24		12	22	22	21	20
13	31	28	28	27		13	24	23	23	21
14	35	33	31	28		14	27	26	26	23
15	40	38	36	32		15	30	29	28	24
16	44	42	39	35		16	35	31	30	27
17	50	45	43	39		17	41	36	35	32
18	57	52	51	47		18	43	38	37	34

10 C is not uniform but declines gradually, resulting in a progressive relative delay in reaching these later stages at higher temperatures.

Information concerning hatching times in the various lots of brook trout embryos is presented in Table V. Increased temperature hastened the onset

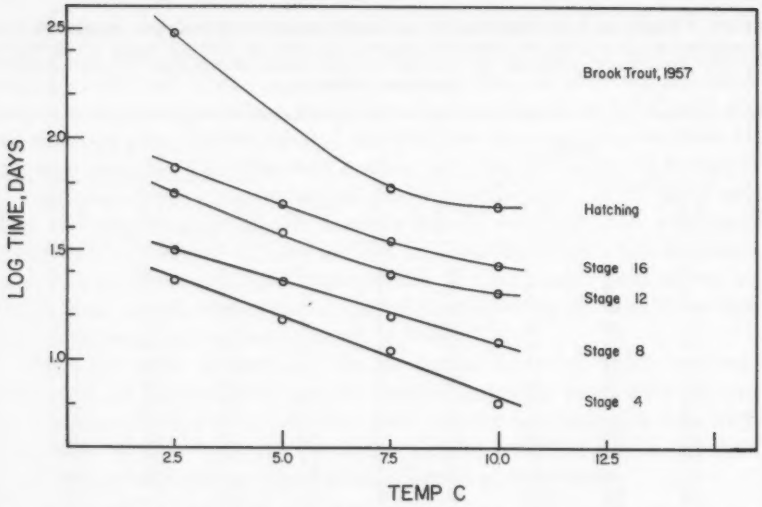

FIG. 1. The effect of temperature on the time required by the control lots of embryos of brook trout to reach four selected developmental stages and on the time of hatching. The lines for stages 4 and 8 are approximately linear and so conform more or less to the rule of Van't Hoff. The other three lines are curvilinear and thus do not conform to that rule.

TABLE V. Hatching times, in days, for the lots of brook trout which were incubated in the 1957 experiment. Incubation time is taken as the time from fertilization to, and including, the median hatching day in the hatching period.

Temp (*C*)	Oxygen (*ppm*)	Beginning of hatch	Hatching period	Median day	Incubation time
2.5	2.6	109	45	31	139
	3.7	111	38	28	138
	4.5	113	34	25	137
	10.5	99	43	31	130
5.0	2.6	83	27	20	109
	3.6	79	30	19	97
	4.4	77	26	19	95
	10.4[a]	73	–	–	–
7.5	2.6	64	23	13	76
	3.4	64	20	8	71
	4.3	63	17	8	70
	10.3	54	14	7	60
10.0	2.5	49	18	9	57
	3.3	49	16	7	55
	4.2	48	8	4	51
	10.2	44	11	7	50

[a]Accidently lost before hatching was completed.

of hatching and reduced the duration of the hatching period which in turn reduced the length of the period of incubation as previously defined. In the control lots the onset of hatching varied from 99 days after fertilization at 2.5 C to 44 days at 10 C. In these lots the hatching period varied in length from 43 days with 31 as its median day at 2.5 C to 11 days with 7 as its median day at 10 C. The corresponding periods of incubation ranged from 130 days at 2.5 C to 50 days at 10 C. The influence of temperature on the time of hatching for brook trout embryos is shown in Fig. 1.

RAINBOW TROUT

The general aspects of the preceding account of the changes in the velocity of development of brook trout embryos incubated at various temperatures are also applicable to rainbow trout embryos. Data for the times taken by the various lots of embryos to reach the selected developmental stages in the 1958 experiment are presented in Table VI. The results of the 1959 experiment are given in Table VII. The times required by the embryos to reach stage 18 varied from 93 days at 2.5 C to 14.5 days at 17.5 C at levels of oxygen approaching air-saturation. The relation of the rate of development to temperature is shown in Fig. 2.

As in the experiment with brook trout, increased temperature accelerated the time of hatching. The onset of hatching varied from 95 days in the control lot at 2.5 C to 29 days at 10 C and to 17 days at 17.5 C. The lengths of the incubation periods for the same spread of temperatures varied from 106 to 18 days. This information is shown in Table VIII. Figure 2 shows the influence of temperature on the time of hatching.

Effects of Oxygen on Developmental Rate and Hatching

BROOK TROUT

The data in Table IV show that in every instance, after the earlier stages had been passed, embryos which developed in an hypoxial environment showed a delay in reaching the specified stages when compared with the appropriate control lot incubated at a level of oxygen near air-saturation. The extent of the delay increased with the reduction of the concentration of dissolved oxygen within any level of temperature. The extent of the delay relative to the appropriate controls also increased with increasing temperature at any one of the three levels of hypoxia. The delay in attaining stage 18 which was caused by the lowest level of oxygen is 11 days at 2.5 C and 9 days at 10 C, but the relative delay is almost three times as great at 10 C. Figure 3 illustrates the influence of the lowest level of oxygen employed (2.5 ppm) on the velocity of development of embryos of brook trout which were incubated at the various temperatures.

Reduced levels of oxygen delayed the time to hatching as well as the appearance of the various developmental stages. These hatching times are shown in Table V. The extension of the time of incubation, based on the

TABLE VI. Times, in days, required by the lots of rainbow trout embryos, incubated at four temperatures and four levels of dissolved oxygen, to reach the 18 selected stages of development in the 1958 experiment. Columns are headed by mean dissolved oxygen levels expressed as parts per million.

	2.5 C				5.0 C		
Stage	2.9	–	11.3	Stage	2.8	3.9	11.3
1	4		4	1	3	3	3
2	8		8	2	7	7	7
3	18		18	3	11	11	11
4	25		25	4	14	14	14
5	28		28	5	16	16	15
6	31		31	6	17	17	16
7	33		33	7	19	19	17
8	35		35	8	20	20	19
9	41		41	9	27	26	25
10	44		44	10	29	28	27
11	47		47	11	31	30	28
12	49		49	12	32	32	29
13	54		54	13	34	33	30
14	64		63	14	43	41	37
15	74		71	15	48	44	40
16	78		75	16	51	49	43
17	88		83	17	57	53	50
18	97		93	18	69	66	59

	7.5 C				10.0 C		
Stage	2.6	3.7	10.6	Stage	2.5	3.5	10.5
1	2	2	2	1	2	2	2
2	4	4	4	2	4	4	4
3	8	7	7	3	6	5	5
4	9	8	8	4	7	6	6
5	10	9	9	5	8	7	7
6	11	10	10	6	9	8	8
7	12	11	11	7	10	9	9
8	13	12	12	8	11	10	10
9	17	17	14	9	14	14	11
10	20	19	15	10	15	15	12
11	22	21	16	11	17	16	13
12	23	22	17	12	18	17	14
13	25	23	18	13	19	18	15
14	29	28	22	14	23	20	17
15	32	30	23	15	28	22	18
16	35	33	26	16	31	24	19
17	41	36	30	17	36	27	23
18	51	46	39	18	39	35	31

median day of hatching during the hatching period, was 9 days or 7% at 2.5 C; at 10 C the extension was 7 days or 14% of the incubation period.

RAINBOW TROUT

The retarding effect of reduced concentrations of dissolved oxygen on the developmental rate of the rainbow trout is apparent at about the same

TABLE VII. Times, in days, required by the lots of rainbow trout embryos to reach the 18 selected stages of development when incubated at oxygen levels approaching air-saturation, at various temperatures. The figures for the lots from 2.5 to 10 C are from Table V and are repeated to facilitate comparison with the figures for lots incubated at oxygen levels approaching air-saturation at temperatures of 12.5–17.5 C in the 1959 experiment.

	Temperature (*C*)						
Stage	2.5	5.0	7.5	10.0	12.5	15.0	17.5
1	4	3	2	2	1.5	1	1
2	8	7	4	4	2.5	2	1.5
3	18	11	7	5	4	3	2.5
4	25	14	8	6	5	4	3
5	28	15	9	7	5.5	4.5	3.5
6	31	16	10	8	6	5	4
7	33	17	11	9	6.5	5.5	4.5
8	35	19	12	10	7	6	5
9	41	25	14	11	9	6.5	5.5
10	44	27	15	12	9.5	7	6
11	47	28	16	13	10	7.5	7
12	49	29	17	14	10.5	8	7.5
13	54	30	18	15	11.5	9	8
14	63	37	22	17	12.5	10	9
15	71	40	23	18	14	11	10
16	75	43	26	19	15.5	13	10.5
17	83	50	30	23	17	15.5	13.5
18	93	59	39	31	18	16.5	14.5

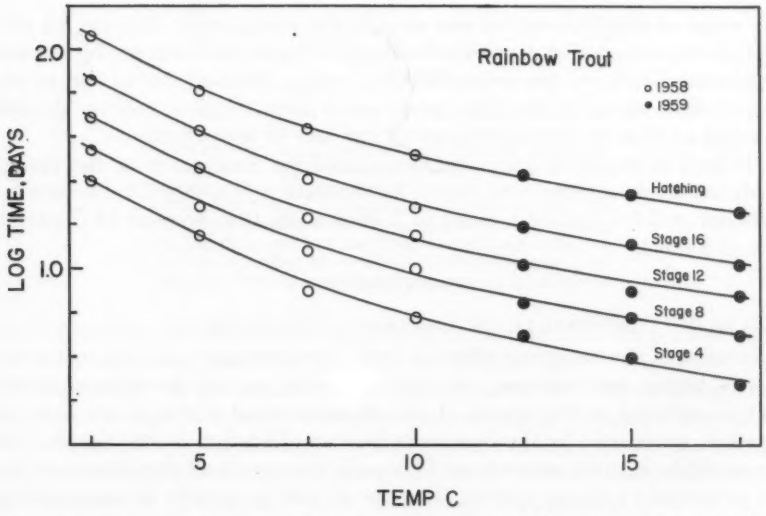

FIG. 2. The effect of temperature on the time required by the control lots of rainbow trout embryos to reach four selected developmental stages and on the time of hatching. None exhibits the linearity required by the rule of Van't Hoff. The lots of embryos in the 1959 experiments (closed circles) were obtained from a different parental population.

TABLE VIII. Rainbow trout hatching times, in days. The figures for temperatures from 2.5 to 10 C are from the 1958 experiment and the figures for temperatures from 12.5 to 17.5 C were obtained from the 1959 experiment. Incubation time is taken as the time from fertilization to and including the median hatching day in the hatching period.

Temp (*C*)	Oxygen (*ppm*)	Beginning of hatch	Hatching period	Median day	Incubation time
2.5	2.9	98	21	11	108
	11.3	95	24	12	106
5.0	2.8	67	15	9	75
	3.9	66	11	7	72
	11.3	58	15	6	64
7.5	2.8	46	13	8	53
	3.7	47	9	6	52
	10.6	38	9	7	44
10.0	2.5	37	12	3	39
	3.5	33	10	5	37
	10.5	29	7	5	33
12.5	9.8	23.5	6	4.5	27
15.0	9.3	19	5	3	22
17.5	9.0	17	3	2	18

early stage of development as was seen in the brook trout. The degree of the effect of hypoxia, which is shown in Table VI, was accentuated by increased temperature. At 2.5 C the lowest level of oxygen delayed the advent of stage 18 by 4 days while at 10 C the delay was 8 days. Figure 3 shows the effect of oxygen in relation to temperature on the rate of development.

Delays in hatching were also occasioned by incubation of the embryos in reduced levels of oxygen as shown by the data in Table VIII. The low level of oxygen at 2.5 C caused a delay of 3 days while that level at 10 C caused a delay of 8 days.

DISCUSSION

EFFECTS OF TEMPERATURE ON EMBRYONIC DEVELOPMENT

Studies of the retarding effect of lower temperatures and the accelerating effect of higher temperatures, in absolute terms, on the developmental rate, which is reflected in the length of the developmental period, have been considered so generously in the literature that amplification of the detail at this time would be entirely redundant. Thorough discussions of this literature have been presented by Hayes (1949), Hayes et al. (1953), and by Kinne and Kinne (1962) who have reviewed the more recent work in this area.

The generalization in the review of Kinne and Kinne, that developmental rate is not a linear function of temperature throughout the biokinetic range

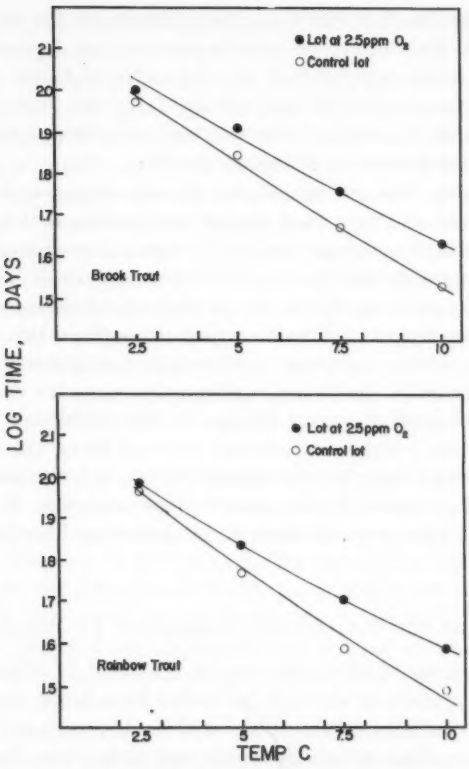

FIG. 3. The effect of the level of dissolved oxygen on the times required by the lots of brook trout embryos and the lots of rainbow trout embryos incubated in hypoxial conditions (approximately 2.5 ppm oxygen). The corresponding control lots were incubated at levels of approximately 10 ppm oxygen. All points are based on the time required to attain stage 18. The divergence of the lines, in each case, indicates that the retarding effect of a particular hypoxial level increases with increased temperature of incubation.

of developmental temperatures, is supported by the data in the present study. When such rates (reciprocals of appropriate units of time) for a broad range of developmental temperatures are arranged graphically the resulting curve is an elongate sigmoid. Some investigators, including Johansen and Krogh (1914), Hayes (1949), Seymour (MS, 1956), and Garside (1959), have tended to ignore the inflections of such a curve and to consider only the central, linear segment of the curve, which they have extrapolated linearly to the x-intercept to determine empirically the temperature of *developmental* or *physiological zero*. Actually the true x-intercepts for their data would be further to the left than those obtained by linear extrapolations of the central segments.

In most instances for fish embryos the x-intercepts for the sigmoids are a few degrees below the freezing point of water and are, in consequence, theoretical points, the lethal temperature for the embryos being somewhat higher. The use of the developmental zero obtained by the linear extrapolation of the central segment to obtain "day-degrees" or other combination of units of time and of temperature is, therefore, invalid.

Further to this, the relationship of the developmental rate of embryos of fishes to the rule of Van't Hoff should be considered. Figures 1 and 2 are essentially Van't Hoff analyses and since the relationships, except possibly for the earlier stages of the development of brook trout, are not linear the rule of Van't Hoff is not applicable. Since the rate of change of developmental rate is not a linear function of temperature throughout the range of developmental temperatures the use of two or more equal products of time and temperature, from two or more developmental temperatures, to define two or more respectively equal proportions of change in development, is also improper. Such misuse of equal numbers of thermal units as being the criterion of equal proportions of development occurs repeatedly through the pertinent literature concerning the experimental treatment of fish embryos. Equal proportions of structural development would seem to be determined by the use of morphological criteria.

Effects of Dissolved Oxygen on Embryonic Development

Pertinent reviews of the influence of the level of dissolved oxygen on the rate of development of embryos of fishes have been provided by Kinne and Kinne (1962) and by Silver et al. (1963). There is universal agreement among the various data which demonstrates that lower levels of dissolved oxygen cause reductions in the developmental rate. The results obtained in the present study further confirm that the concentration of dissolved oxygen markedly influences the rate of development and the times of hatching of embryos of brook trout and rainbow trout as has been found in all other species tested.

Figure 3 shows that for a specified level of hypoxia there is a progressive increase in the relative effect with increasing temperature. This progressive retardation in development has been demonstrated previously in other species by Lindroth (1942, 1946), Einsele (1956), Alderdice et al. (1958), and Garside (1959). Furthermore, the onset of the delay in development also occurs at progressively earlier stages with increasing temperature, presumably as a result of the higher metabolic need for oxygen with increasing temperature. For instance, Table VI shows that in embryos of rainbow trout, at 2.5 C, the metabolic requirements were satisfied by a level of approximately 2.9 ppm of oxygen, relative to the control embryos at 11.3 ppm of oxygen, until just before the formation of pigment in the iris (stage 13). However, at 10 C there is some suggestion of a limiting effect at 2.5 ppm of oxygen as early as stage 3, the earliest appearance of axiation. Such retardation becomes rapidly greater

following the closing of the blastopore (stage 8). These findings parallel those by Garside (1959) for lake trout. However, the rates of development have not been as severely affected in brook trout and rainbow trout as in lake trout. Levels of 2.5 and 3.3 ppm of oxygen at 10 C induced teratologic development and eventual mortality in all embryos of lake trout whereas abnormal development of embryos of brook trout and rainbow trout was less frequent and some embryos of normal appearance developed in every hypoxial environment. Silver et al. (1963) have discussed the apparent ability of embryos of at least some species of fish to compensate for reductions in ambient oxygen by concomitant reduction in the pace of developmental metabolism which is reflected in retarded but otherwise normal development. They show survival of embryos of rainbow trout and of chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), at least for a short period beyond hatching (experiment deliberately terminated) at levels as low as 2.5 ppm of oxygen, in a variety of velocities of waterflow. However, there was total mortality in all lots of both species at 1.6 ppm of oxygen.

The apparent levels of oxygen required for survival by developing embryos of salmonid fishes as indicated by the results of Silver et al. (1963), Garside (1959), and by the information in the present study are considerably lower than the levels (from 5.6 to 7.2 ppm, during the second half of the embryonal term) predicted by Alderdice et al. (1958), using mathematical models provided by Krogh (1941), for chum salmon *Oncorhynchus keta*. Silver and coworkers have justifiably criticized the impropriety of the use of such models since the form of the embryos fails completely to satisfy the assumptions upon which these formulas are based.

Comparisons of the size of newly hatched alevins of the various experimental lots were not made in the present study. However, Silver et al. (1963) report considerable differences in the mean lengths of newly hatched alevins from the various lots as a result of the treatment of these embryos with various levels of dissolved oxygen at several velocities of waterflow. Mean length increased with increasing levels of dissolved oxygen at any selected velocity and similarly, mean length increased with increasing velocity at any selected level of oxygen. These results are of rather special interest since they are in contrast with those obtained when the developmental rate is controlled by temperature as first shown by Gray (1928). Those embryos which develop most rapidly, that is at higher temperatures, are shorter at the time of hatching than those of the same species which are incubated at lower temperatures. The reasons for these opposite effects induced by temperature on one hand and by the supply of oxygen on the other while both affect the apparent developmental rate in the same direction as demonstrated in the present work are completely obscure.

ACKNOWLEDGMENTS

I wish to express my thanks to Dr F. E. J. Fry, Department of Zoology, University of Toronto, who suggested the study and who provided much

counsel during its execution. Financial assistance was provided by grants to Dr Fry from the Ontario Research Foundation and the National Research Council, through the University of Toronto Research Committee. Facilities for these experiments were provided by the Research Branch of the Ontario Department of Lands and Forests at the Laboratory for Experimental Limnology, Maple, Ont. Trout eggs were provided bv the Fish and Wildlife Branch of that Department.

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Depth Distribution of Oceanic Shrimps (Decapoda; Natantia) off Oregon[1]

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ABSTRACT

Sixteen species of oceanic shrimps, seven Penaeidea and nine Caridea, appeared in 244 collections made within the upper 1500 m at one station In the northeast Pacific off Oregon. Most of the species were primarily mesopelagic in distribution.

The most abundant species, *Sergestes similis*, was the only shrimp common in epipelagic waters at night and the only species clearly demonstrating diel vertical migrations. Night catches exceeded day catches in near-surface waters, while day catches exceeded night catches at mid-depths. *Sergestes similis* migrated into the upper 50 m at night and on one occasion was collected at the surface.

INTRODUCTION

Nektonic shrimps often comprise a significant portion of the biomass of midwater collections from the open ocean and the deep sea. Sergestids, for example, may be so abundant that they are suspected to cause sonic scattering layers in the ocean (Barham, MS, 1957, 1963). There is a commercial fishery for *Sergestes* in Japan (Yaldwyn, 1957).

Important studies of vertical distribution of oceanic and deep-sea shrimps include Waterman et al. (1939), Welsh et al. (1937), Sund (1920), Stephensen (1923), and Murray and Hjort (1912). None of these studies was made in the Pacific Ocean.

The cruises of the *Albatross* have provided material for several reports on penaeid and carid shrimps from the northeastern Pacific (Faxon, 1895; Rathbun, 1910; Schmitt, 1921). Since most of these collections were made with bottom trawls on the continental shelf, little about the vertical distribution of oceanic species can be concluded.

In this paper we present data on the vertical distribution of oceanic shrimps found off the coast of Oregon. Specimens were collected from the

[1]Received for publication February 4, 1966.

J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

upper 1500 m of water mainly at one station over a period of 3 years. Forss (MS, 1965, and unpublished data) discusses the systematic relationships of these species. The distribution of other small nektonic animals (fishes and squids) has been reported by Pearcy (1964, 1965) and Pearcy and Laurs (1966).

METHODS

Shrimps were collected mainly from a single station located about 50 miles off the central Oregon coast (44°39′N, 125°15′W) from the R/V *Acona*. This location is just beyond the continental slope where the water depth is about 2000 m. Collections were made in daylight and darkness during all seasons of the year from June 1961 through September 1964.

Eighty-two collections were made with a 6-ft Isaacs-Kidd midwater trawl. These collections were taken to depths of approximately 200, 500, and 1000 m using the methods described by Pearcy (1964). The front half of this net consisted of a 76-mm stretch mesh, the after half was lined with 13-mm stretch mesh, and the codend was a ½-m plankton net (0.571-mm mesh aperture).

Forty-five tows were made with an Isaacs-Kidd midwater trawl modified to capture animals within three depth strata during one oblique tow. The conventional 6-ft trawl was adapted with a multiple plankton sampler (Bé, 1962) as an opening and closing codend unit (Pearcy and Hubbard, 1964). This unit was calibrated to sample from 0 to 150, 150 to 500, and 500 to 1000 m (Pearcy and Laurs, 1966). A depth-distance recorder provided estimates of the volume of water filtered within each depth stratum. This net was lined throughout with a 10-mm stretch mesh.

Plankton nets, 1 m in diameter (mesh aperture 0.571 mm), were used to collect 99 samples. Pressure-actuated wire cutters (Yentsch et al., 1962), calibrated by lowering vertically at sea, were used to open and close the nets. Nets were fished in tandem providing samples from depths of 0 to 150, 150 to 500, 500 to 1000, and 1000 to 1500 m.

In addition to these collections we made 18 horizontal midwater trawl tows at night at various depths within the upper 200 m. Five of these tows were made at another station 25 miles west of the mouth of the Columbia River.

All samples were preserved at sea with 10% buffered formalin. Shrimps were counted and identified in the laboratory ashore.

RESULTS AND DISCUSSION

Vertical Distribution

No species of shrimp was captured exclusively within the upper 200 m with any type of net (Table I). Eight species were captured within the upper 200 m as well as within deeper layers: *Sergestes similis*, *Pasiphaea pacifica*, *P. chacei*, *Petalidium suspiriosum*, *Hymenodora frontalis*, *H. gracilis*, *Systellaspis braueri*, and *Bentheogennema* sp. Of these, only *Sergestes similis*, by far

the most abundant species, was captured in large numbers within the epipelagic or surface waters; this was only during the night. *Pasiphaea pacifica* and *P. chacei* were rare in the collections at this station, although they have been captured frequently in 0–200-m tows elsewhere off Oregon (Forss and Pearcy, unpublished data).

Some of the above species, although present, were uncommon in collections from epipelagic waters. Judged from the distribution of catches, especially in the nonclosing net, *Petalidium suspiriosum*, *Hymenodora frontalis*, *H. gracilis*, *Systellaspis braueri*, and *Bentheogennema* sp. were most abundant below 200 m (Table IA). A few of the individuals found in the upper net of the opening-closing codend of the midwater trawl (Table IB) may be contamination from previous tows in deeper water.

Eight species were never captured in tows confined to epipelagic waters. *Bentheogennema borealis*, *Notostomus japonicus*, *Gennadas propinquus*, and *Acanthephyra curtirostris* were found only in tows that fished below 150–200 m. *Parapasiphaë sulcatifrons*, *P. cristata*, *Sergia tenuiremis*, and *Gennadas incertus*, though few in numbers, were captured only in nonclosing tows to depths of 1000 m or opening-closing tows at 500–1000 m.

Thus, from our collections we can construct a generalized table of vertical distribution as follows:

EPIPELAGIC (0–200 m) only

None

EPIPELAGIC (0–200 m) and MESOPELAGIC (200–1000 m)

Sergestes similis
Pasiphaea pacifica
Pasiphaea chacei

MESOPELAGIC (200–1000 m)

200–1000 m mainly
Petalidium suspiriosum
Hymenodora frontalis
Hymenodora gracilis
Systellaspis braueri
Bentheogennema sp.
200–1000 m only
Notostomus japonicus
Bentheogennema borealis
Gennadas propinquus
Acanthephyra curtirostris
500–1000 m only
Parapasiphaë sulcatifrons
Parapasiphaë cristata
Sergia tenuiremis
Gennadas incertus

This arrangement is tentative, especially for the lower mesopelagic shrimps that were rarely captured. Moreover, the distribution of mesopelagic species may obviously extend into bathypelagic depths below 1000 m.

Some morphological and distributional evidence can also be cited to support the conclusion that the penaeid *Sergestes similis* and the carids *Pasiphaea pacifica* and *P. chacei* are shallow in distribution compared to the other species. They are nearly transparent when alive. Only the "organ of Pesta" in the cephalothorax of *S. similis* is densely pigmented. The deeper shrimps, on the other hand, are all more extensively pigmented. Our *Hymenodora* spp. are orange, and the other mesopelagic species are a deep red or scarlet, typical colorations for mesopelagic and bathypelagic shrimps (Faxon, 1895; Murray and Hjort, 1912; and Marshall, 1954). Also, *S. similis* and *P. pacifica* are common in midwater collections over the continental shelf or inner slope off Oregon (Forss and Pearcy, unpublished data) indicating that these species occur in fairly shallow waters. Moreover these two species have been collected in the northeastern Pacific where the depth of the bottom was less than 300 m, while *A. curtirostris* and *H. frontalis* were captured only where the water depth was 589 m or more (Schmitt, 1921).

Two species of shrimps collected off Oregon were also included in Tchindonova's (1959) account of the depth distribution of macroplankton from the northwestern Pacific. She reported *Sergestes similis* within the upper 1000 m with a center of abundance between 100 and 500 m. *Hymenodora frontalis* had a wide depth distribution between about 200 and 3000 m with a center of abundance between 500 and 1000 m. Thus our results agree with hers for these species.

Vertical Migrations

Vertical migrations of *Sergestes* have been reported by Welsh et al. (1937), Sund (1920), Yaldwyn (1957), and Waterman et al. (1939). Differences between our catches made at night and those made during the day with the opening-closing nets demonstrate that *S. similis* also undertakes diel vertical migrations. In the upper 150 m more *S. similis* were always caught in the midwater trawl at night than during the day (Fig. 1 and Table I). Between 150 and 500 m catches were usually higher during the day than the night. These opposite trends at surface and mid-depths indicate diel vertical movement. Although *S. similis* frequently occurred in the 500–1000-m stratum, their density in deep water was lower than in overlying waters. An exception was the capture of 174 animals in a 500–1000-m day tow (for XI in Fig. 1). Consistent day–night differences, however, were not apparent in deep water. Similarly, the catches of *S. similis* in the meter net showed distinct diel variations above 500 m and were low below 500 m (Table IC).

Day–night differences are evident from the 0 to 200-m nonclosing midwater trawl collections (Table IA); here the catch per hour during the night was also many times higher than that made during the day. Trends are not

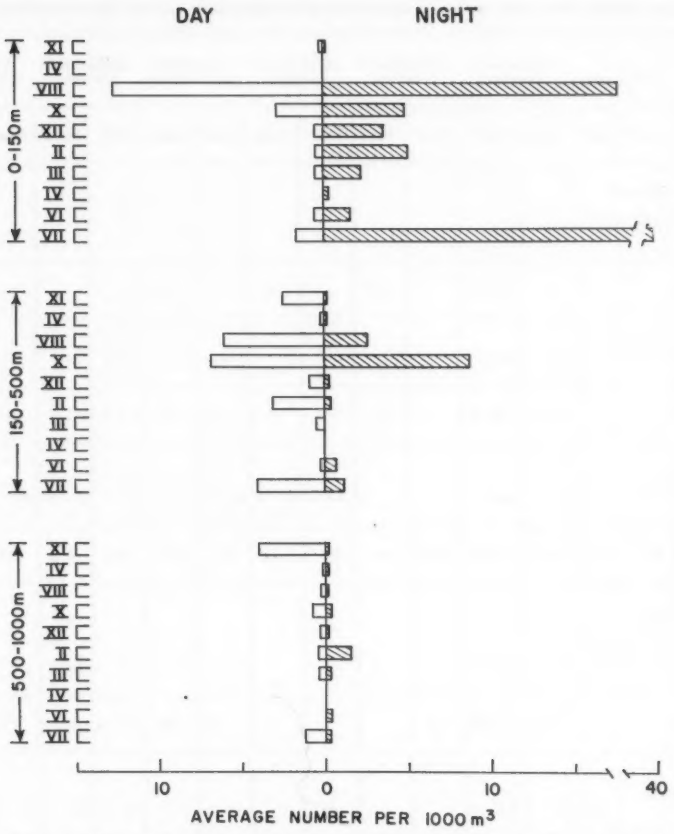

FIG. 1. Vertical distribution of *Sergestes similis* during day and night periods at three depths. Each horizontal bar represents an average monthly catch made with the midwater trawl and opening and closing codend device at the station 50 miles west of Newport, Oregon. Roman numerals designate months, November 1962 to July 1964.

evident in the 0–500-m tows, however, probably because the trawl sampled continuously and because the population simply moved up and down within this zone.

Our study provides no similar evidence for vertical migrations of other species, but conclusions cannot be made because the catches were small.

UPPER DEPTH DISTRIBUTION OF *SERGESTES SIMILIS*

Three series of stratified, nonclosing midwater collections made at various depths in the upper 200 m provided information on the upper depth range of *S. similis* at night (Table II). In August 1961, *S. similis* was collected in all

TABLE I. Catches of oceanic shrimps in collections to various depths within the upper 1500 m at a station off Newport,

	Sergestes similis		*Pasiphaea chacei*		*Pasiphaea pacifica*		*Petalidium suspiriosum*		*Hymenodora frontalis*		*Bentheogennema* sp.		*Systellaspis braueri*	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
A. Nonclosing midwater trawl														
0–200 m (32 collections) Total No.	26	3829		4		1		1						
No. per hour	3.7	273.5		.29		.07		.07						
0–500 m (24 collections) Total No.	1128	1109		2	1	2	10	1	55	53	3	18		5
No. per hour	53.7	52.8		.1	.05	.1	.48	.05	2.6	2.5	.14	.86		.24
0–1000 m (26 collections) Total No.	573	384	1		4	2	120	91	388	273	53	21	24	9
No. per hour	9.4	14.8	.02		.07	.08	2.0	3.5	6.4	10.5	.87	.81	.39	.35
B. Opening-closing midwater trawl														
0–150 m (45 collections) Total No.	232	545					12	1	17	19	1			1
No. /10^3/m^3	1.82	6.05					.09	.01	.13	.21	.01			.01
150–500 m (45 collections) Total No.	614	187					2	1	18	17	1	2		
No. /10^3/m^3	2.35	.89					.01	.004	.07	.08	.003	.01		
500–1000 m (45 collections) Total No.	302	46	1	1	2		8	2	147	86	11	11		3
No. /10^3/m^3	.80	.15	.002	.003	.005		.02	.01	.39	.29	.03	.04		.01
C. Opening-closing meter nets														
0–150 m (37 collections) Total No.	3	50												
150–500 m (32 collections) Total No.	48	13								2	1			
500–1000 m (22 collections) Total No.	3	2					3		7	2		1	1	
1000–1500 m (8 collections) Total No.									1	1				1

Oregon, 1961–64. The species are listed in order of vertical distribution on the basis of data from the nonclosing midwater trawl.

Notostomus japonicus		*Gennadas propinquus*		*Hymenodora gracilis*		*Bentheogennema borealis*		*Parapasiphaë sulcatifrons*		*Parapasiphaë cristata*		*Acanthephyra curtirostris*		*Sergia tenuiremis*		*Gennadas incertus*	
Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
1		1	1														
.05		.05	.05														
3	2			92	15	5	2	4	2	1	1	2	2	1	2	1	
.05	.08			1.5	.58	.08	.08	.07	.08	.02	.04	.03	.08	.02	.08	.02	
				3	1												
				.02	.01												
1							1					1					
.003							.004					.003					
				2	1	1	2						1	1	2	1	1
				.005	.003	.002	.01						.003	.002	.01	.002	.003
						1											

TABLE II. Catches of *Sergestes similis* in horizontal tows at various depths within the upper 200 m during the night at two stations, assuming a 4:1 cable to depth ratio.

Maximum depth (*m*)	Total No.	No. per hour	Location, time, and conditions
Surface	95	211.1	50 miles off Newport
15	2327	5411.6	0156–0330 PST
25	470	626.6	August 9, 1961
50	217	380.7	overcast – rain
100	225	357.1	
200	146	158.6	
Surface	0	0.0	50 miles off Newport
10	140	424.0	2214–0154 PST
25	136	340.0	February 26, 1962
50	381	952.5	no moon
100	129	258.0	
150	106	185.9	
200	52	91.2	
Surface	0	0.0	25 miles off Columbia River
10	0	0.0	0007–0427 PST
20	0	0.0	September 19, 1962
50	270	642.8	moon visible
200	127	204.8	

tows from the surface to 200 m. Highest catches were at 15 m. In February 1962, no *S. similis* was taken at the surface, and peak concentrations were taken at 10–50 m. In September 1962, *S. similis* was not captured within the upper 20 m but only occurred in the 50- and 200-m tows. The clear night and moonlight probably affected the ascent of animals during this latter series of tows. These limited data show that the upper depth distribution of *S. similis* is variable. They ascend into the upper 50 m at night, well above the base of the halocline (100–200 m), and sometimes into the summer thermocline (10–50 m) as well.

ACKNOWLEDGMENTS

This research was supported by Atomic Energy Commission Contracts No. AT(45-1)1726 and AT(45-1)1750. We wish to thank C. N. Mooers and R. M. Laurs for translating the Russian paper.

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Biology of the Atlantic Argentine (*Argentina silus* Ascanius) on the Scotian Shelf[1]

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ABSTRACT

On the Scotian Shelf, *Argentina silus* Ascanius was found mainly along the continental slope but extended into the deep-water basins of the central shelf. It was not found in the Bay of Fundy, and only a few were found in the Gulf of St. Lawrence. It was found in largest numbers in depths between 100 and 150 fath (183–275 m) and at temperatures between 4 and 10 C.

Although larger fish were usually found deeper, in general argentines from the slope region had a modal length of 21–28 cm and were from 2 to 7 years of age. Argentines taken from Emerald Basin had a modal length of 18–22 cm and were 1 or 2 years of age in autumn, but had a modal length of 30–36 cm and were 6–11 years of age in winter.

Spawning occurred in the spring in Emerald Basin with males maturing around 25 cm and females around 30 cm.

Since argentines grow slowly after the first few years and do not mature until several years after growth slows down, it is possible that heavy fishing might quickly reduce stocks and catches below current levels.

INTRODUCTION

The atlantic argentine, *Argentina silus* Ascanius, is a small-mouthed, silvery-coloured, smelt-like fish with a slender body and large eyes (Fig. 1). Two species of the genus *Argentina* occur in the western North Atlantic, *A. silus* and *A. striata* (Goode and Bean, 1896). *Argentina striata* is a more southern species, common in the Gulf of Mexico and Tortugas area (Springer and Bullis, 1956), but has been reported from off southern Nova Scotia (Schroeder, 1955). *Argentina silus* is the common species recorded from the Gulf of Maine and eastern seaboard of Canada (Bigelow and Schroeder, 1953), and was the only species of *Argentina* seen in our survey catches.

Populations of *A. silus* are reported from both sides of the North Atlantic (Cohen, 1958) as well as in the Iceland area (Fridriksson, 1937). Borodulina (1964) records argentines off the southern part of both the east and west coasts of Greenland as well. On the eastern side of the Atlantic the southern limits of distribution are near 49°N (just south of Ireland). To the north, argentines are common off the coast of Norway and in the southwestern part of the Barents Sea (Borodulina, 1964) and penetrate with the warm water up to the southwest coast of Spitzbergen (Maslov, 1944).

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J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

On the western side of the Atlantic, the southern end of the range for *Argentina silus* lies near Cape Cod (Cohen, 1958), with fishable concentrations reported on Georges Bank (Firth, 1931). According to Borodulina (1964), it is common north to the Grand Bank of Newfoundland.

The argentine is not well known to North American fishermen because it escapes through the large-mesh nets currently used by most. It was recorded occasionally from Nova Scotian banks (McKenzie and Homans, 1937; McKenzie, 1939) and from Georges Bank (Firth, 1931). However, Bigelow and Schroeder wrote in 1953 that nothing was known of the life history of argentines in the Gulf of Maine. A similar statement could have been made for the whole of the Northwest Atlantic.

Development by European countries of small-mesh otter-trawl fisheries in the Northwest Atlantic for silver hake, *Merluccius bilinearis*, and herring, *Clupea harengus*, has resulted in landings of argentines in considerable quantity. Landings of argentines by the USSR in 1963 were about 12 thousand metric tons; in 1964 landings reached 17 thousand metric tons. It is likely that many argentines were consigned, unidentified, to reduction aboard factory vessels, so landings may have been considerably greater.

Canadian research-vessel surveys with otter trawls partially lined with fine-mesh netting, beginning in 1958, have provided considerable information on distribution of this species within the Canadian region. More recent studies (1964 and 1965) have provided information about growth, age, and size composition of stocks, and stages of maturity. These results are reported in this paper.

METHODS AND MATERIALS

Most information on the distribution of argentines resulted from a series of research-vessel survey cruises conducted from 1958 to the winter of 1965. The area covered extended from Gaspé, in the Gulf of St. Lawrence, southward to the Bay of Fundy (Fig. 2). Two research vessels, the 84-ft (1 ft = 0.3048 m) *Harengus* and the 177-ft *A. T. Cameron*, were used throughout most of this period. In 1964 a 94-ft chartered vessel, the *Alder Point*, was used for two short cruises between September and early October.

Otter trawls were used by all three vessels to carry out the surveys. Details of the gear used by the *A. T. Cameron* and *Harengus* are given by Jean (1964). Briefly summarized, the *Harengus* used a manila or polyethylene trawl with 60-ft headline. The *A. T. Cameron* used a manila or polyethylene trawl with a 79-ft headline. Internal mesh size ranged from about $4\frac{3}{4}$ inches (1 inch = 2.54 cm) in the forward part of the net to about 3 inches in the codend. Throughout the cruises the codend was either lined or covered with $1\frac{1}{8}$-inch netting. The *Alder Point* used a polyethylene trawl similar in dimensions to that of the *A. T. Cameron* during the first cruise but during the second cruise the wings of the net were modified to give a higher headline height. Throughout, the codend was lined with $1\frac{1}{8}$-inch liner.

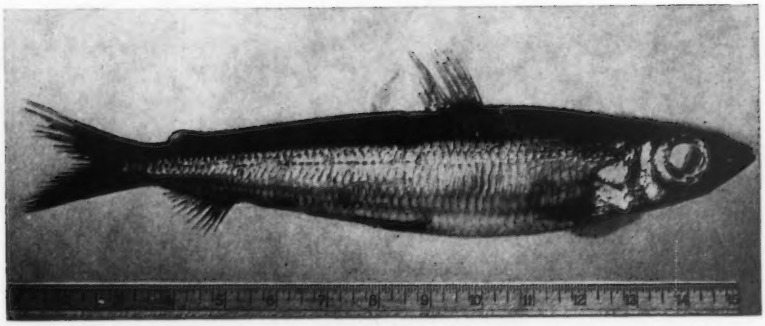

FIG. 1. An argentine, *Argentina silus* Ascanius, about 35 cm in length. (Photo by E. Squires.)

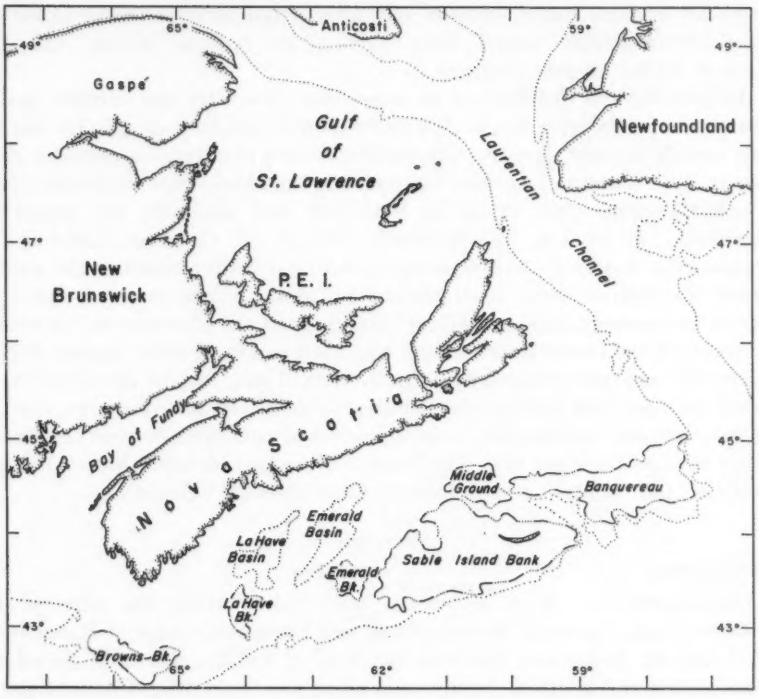

FIG. 2. Map of the area surveyed showing some of the principal banks and the 50- and 100-fath depth contours.

Size of meshes and type of net may be particularly important in recording distribution of argentines. The nets used were designed for species such as cod and haddock and each had large meshes in the wings, square, and belly. These may allow substantial escapement of the slim-bodied argentines. Also, from echo traces in areas where argentines were found, it seems likely they are less closely related to bottom than cod and haddock. Both these circumstances present some limitations to the data.

Argentine catches were sampled with varying thoroughness. In many smaller catches all fish were counted but not measured. Length measurements were made to the nearest centimetre and represent fork length. Large catches were often put in baskets, weighed, and the numbers in a particular volume obtained for conversion. In recent cruises, random or stratified samples were examined for sex, maturity stages, and stomach contents. Otoliths were taken and stored in glycerin for subsequent ageing. Age determinations were made with unbroken otoliths by reflected light under a low power (10 x) dissecting microscope. A hyaline plus an opaque ring were assumed to indicate 1 year in the life of the fish.

At all stations fished, surface and bottom temperatures were taken and a bathythermograph record from surface to bottom above 150 fath (1 fath = 1.8285 m) was obtained.

In plotting the distribution of argentines shown by our catches, several arbitrary decisions were made. We believe that numbers caught by the different vessels are not directly comparable. Conversion factors between *A. T. Cameron* and *Harengus* catches for cod and haddock were available (Jean, 1964; McCracken, 1966, in press) but none was available for argentines. Presumably, as for cod and haddock, the *A. T. Cameron* outfished the *Harengus*. To overcome the problem of different fishing abilities the catches showing distribution have been plotted by season, since most of the *A. T. Cameron* cruises were made in "winter" and those of the *Harengus* in "summer."

Areas off the Canadian mainland had been surveyed with varying degrees of intensity and not necessarily in each year. Thus, to plot distribution, we divided the area into units of 10 minutes latitude and longitude, grouped all tows in a "season" within each unit regardless of year, and derived an average number of argentines per tow. The "summer" season included March through September, the "winter" season from October through February.

RESULTS

Distribution

Geographical. Most argentines were taken along the edge of the continental slope, between Browns Bank and the eastern edge of Banquereau (Fig. 3 and 4). None was taken in the Bay of Fundy, and only occasional specimens east and north of Banquereau along the Laurentian Channel and in the Gulf of St. Lawrence. The most northerly record was of a specimen at 48°50′N, 63°30′W, off Gaspé.

Catches of several thousand argentines per 30-min tow were made in the Emerald Basin area, but catches of this size were recorded more commonly on the seaward side of Sable Island, and Emerald and Browns banks. Although argentines were found along the edge of the continental shelf in both winter and summer, tows in summer took the greatest numbers off LaHave and Emerald banks, while in winter large numbers of argentines were taken both there and to the eastward off Sable Island and the southwestern part of Banquereau.

Our data gathered at various times from 1958 to 1964 indicate that the winter range is more extensive than the summer range. However, a more detailed seasonal survey is needed before this conclusion may be drawn with assurance.

By depth and temperature. Argentines are restricted generally to deeper water, with only occasional specimens occurring in shallow water (Fig. 3 and 4). Our records include captures of three specimens at 28 fath and, at the other end of the range, one specimen at 393 fath. However, the largest catches came consistently from between 100 and 200 fath (Fig. 5). While fishing with the *A. T. Cameron* to 200 fath during summer, the greatest average catch per tow was produced in the range between 100 and 140 fath.

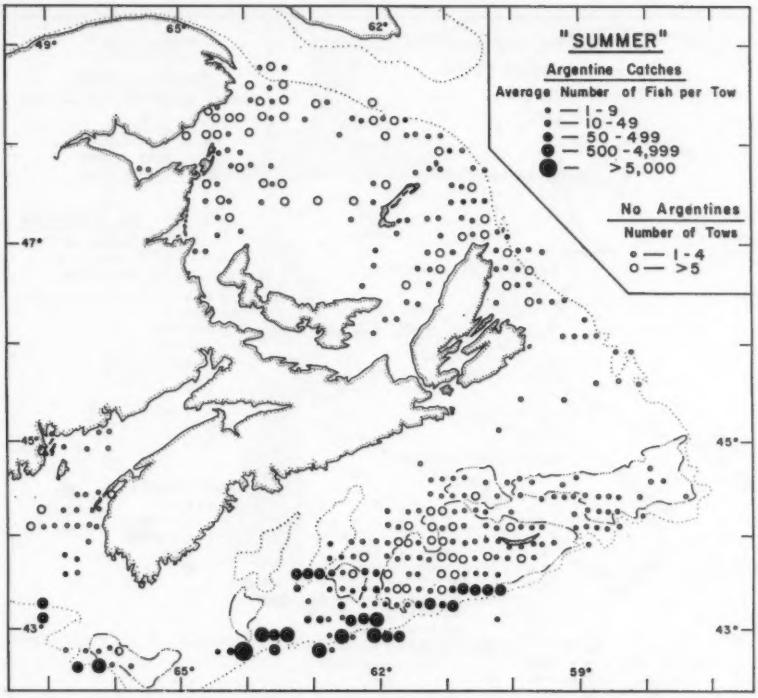

FIG. 3. Distribution of argentines in "summer" 1958–64 as shown by research-vessel otter-trawl catches.

Catch per tow reached a high in the same depth range in winter, although the average number per tow was less. Some fishing with the *A. T. Cameron* in November (several years) over a relatively wider range of depths showed similar depth distribution although best catches of argentines were slightly deeper, around 150 fath.

Cruises in September–October 1964 (*Alder Point*), with most effort concentrated in depths between 75 and 200 fath, gave catches averaging about 4000 fish per hour tow (1000 lb) in the best area at depths between 140 and 160 fath.

Argentines were taken over a wide range of bottom temperatures, from 0 to 11 C, but the temperatures at which they most frequently occurred and largest numbers were caught were about 4–10 C during the period of these surveys (Fig. 6).

BY SIZE. The sizes of argentines caught varied considerably by depth and also by area. A summation of all survey data (for which length composition was available) for the period 1958–64 showed that smallest argentines were taken in the shallowest water and that mean length increased progressively

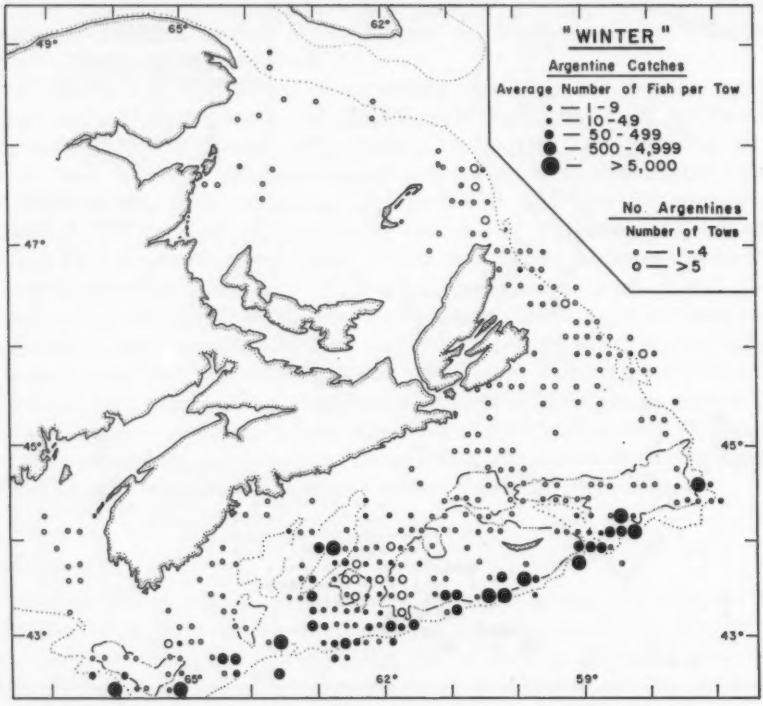

FIG. 4. Distribution of argentines in "winter" 1959–64 as shown by research-vessel otter-trawl catches.

with depth of capture (Fig. 7). At about 50 fath mean length was 21.9 cm while around 130 fath it was 27.6 cm.

During March 1965 fishing along the edge of the shelf off Emerald and LaHave banks provided an opportunity to test these findings by making a series of tows at different depths in one region. Mean length increased from about 21 cm at 70 fath to about 29 cm at 130 fath (Fig. 7). A few argentines (all were over 34 cm in length) were taken in still deeper water, around 195 fath.

Along with this relatively straightforward relationship between length and depth (or some factor such as temperature which is related to depth) within one area, there is a marked difference in lengths and ages of fish taken from different regions. During the fall of 1964 fishing for argentines was carried out along the edge of the Scotian Shelf between LaHave and Emerald banks and in the southwestern part of Emerald Basin. In March 1965 fishing was carried out in about the same region along the Scotian Shelf and in the central part of the Emerald Basin.

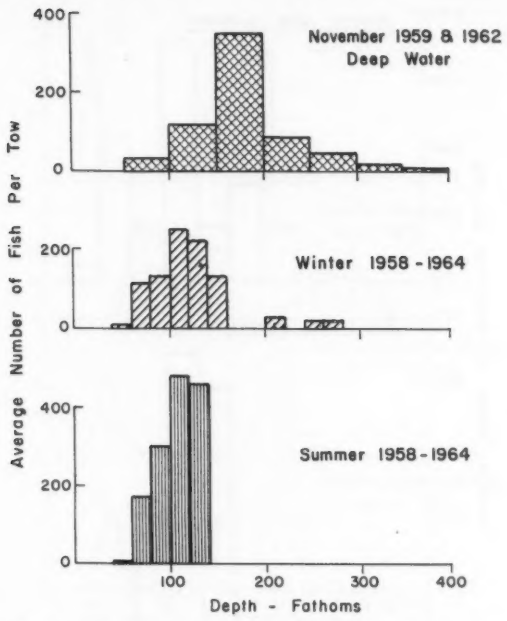

FIG. 5. Catches of argentines in relation to depth of fishing.

Along the edge of the Scotian Shelf, at both seasons, length and age compositions were similar (Fig. 8). Modal length was around 21–28 cm and fish of 3–6 years of age predominated in the catches. However, catches in Emerald Basin were quite dissimilar. In September 1964, catches from the western part of the Basin comprised mainly small argentines, modal length 18–22 cm, in which the 2- and 3-year-old fish predominated. In March 1965, catches from the central part of this basin comprised only larger, older argentines, for which the modal length was 30–36 cm, with fish of 6–11 years of age predominating. Small fish less than 4 years of age were absent.

ASPECTS OF LIFE HISTORY

OTOLITH FORMATION. Examination of otolith characteristics from 472 argentines taken from the Scotian Shelf in September–October 1964 showed that in about 98% of the fish a wide opaque zone (the summer growth increment) characterized the otolith edge. Similar examination of otoliths from 327 argentines taken in March 1965 showed that about 97% had hyaline material (a winter ring) around the outer edge. Thus it appears that the winter ring starts to form on the otolith some time in the fall.

For the European side of the North Atlantic, Borodulina (1964) indicates that a few argentines taken in late April had begun to form summer growth

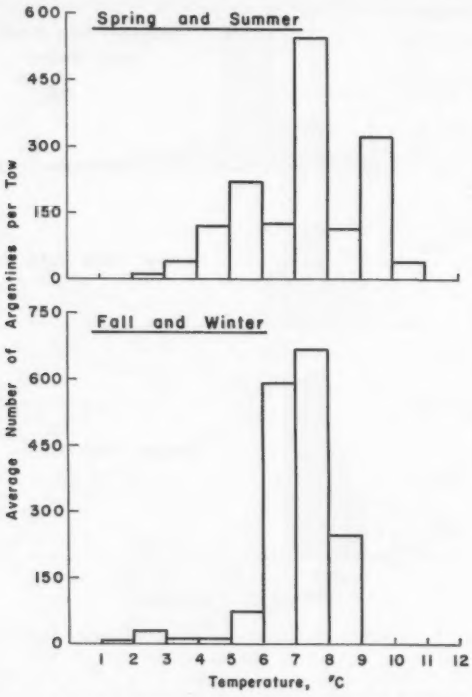

FIG. 6. Numbers of argentines caught in relation to temperature for summer and winter seasons.

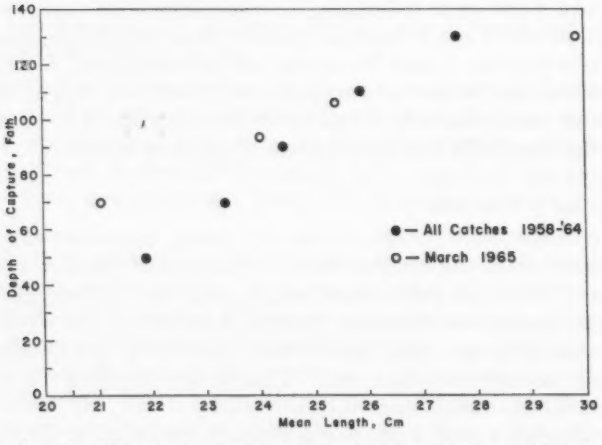

FIG. 7. The relation between mean size of argentines and depth of capture

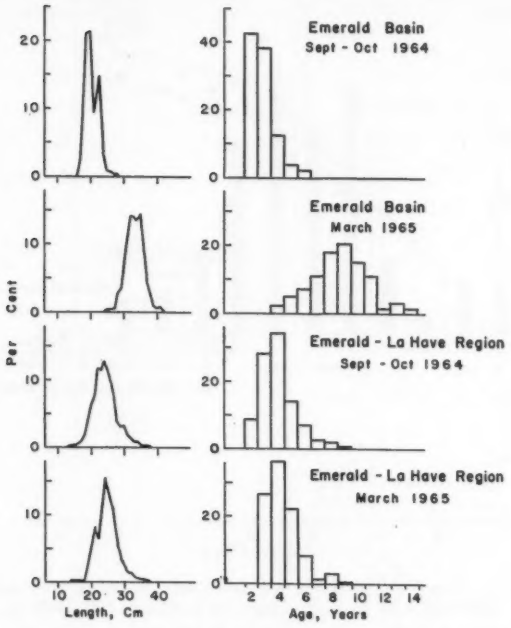

FIG. 8. Lengths and ages of argentines from Emerald Basin and the Emerald–LaHave Bank region of the Scotian Shelf, 1964–65.

on the otolith. Probably the timing of new growth is similar for argentines in the North American region but no precise information is available.

GROWTH. Fish from the Emerald Basin region taken during our survey in March 1965 have been separated by sexes and their length-at-age shown for males and females (Fig. 9). Most were between ages 6 and 11, and throughout this range females were about 2–3 cm longer than males the same age. Argentines in our catches from the edge of the Scotian Shelf were mainly immature and ranged from 2 to 7 years old. Length-at-age of these fish has been shown for the sexes combined.

Argentines in these regions increase rapidly in length during the first years of life, reaching an average length of about 19 cm as 2-year-old fish. Subsequently, growth in length slows considerably; fish of 6 years average about 30 cm and those of 11 years about 35 cm. Annual length increments from 2 to 6 years of age average about 2.5 cm, from 6 to 11 years about 1 cm.

MATURITY. The lengths and ages of the group of ripe and spawning fish encountered in the Emerald Basin region in March 1965 are shown in Fig. 10, separated according to sex. Of the argentines caught, 576 specimens were examined, only two of which were judged to be immature from field examinations. The remainder were in stages from ripening to spawning and

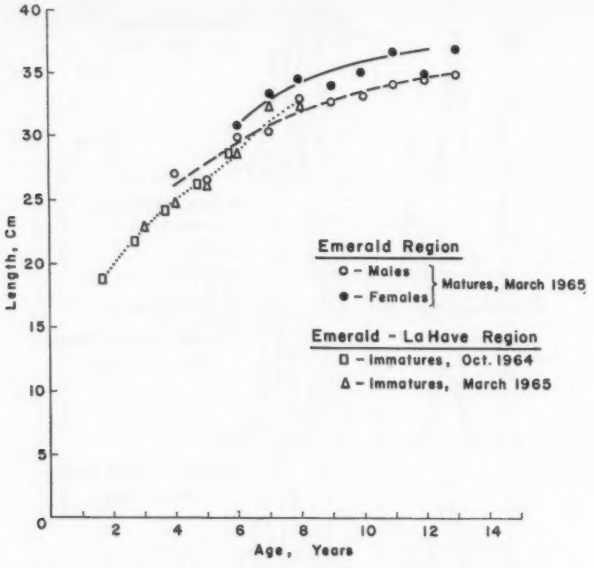

FIG. 9. Mean length-at-age for argentines by sexes for mature fish and with sexes combined for immature fish, 1964–65.

maturity was thus easily recognized. Males began maturing at a slightly shorter length, around 25 cm, and females around 30 cm. This difference in length reflects some differences in age of maturation, with a few mature males being taken at 4 years of age while no mature females were taken before 6 years of age (Fig. 10).

During the March 1965 cruise no other group of argentines was encountered in which mature fish could be distinguished with confidence. Most of those caught along the edge of the continental shelf were less than 30 cm in length and appeared immature.

SPAWNING SEASON. The best data on spawning season obtained during our studies were for argentines taken in Emerald Basin during March 1965 (Table I). Spawning in that region appeared to be just beginning, as about 18% of females and 2% of males were in stage VI (spawning), and about 60% of females and 70% of males were in stage V (ripe or gravid).

The data collected in September–October 1964 on maturity stages are in general agreement with these results. About 70% of the mature females examined from the slope area were in stage III or IV (early ripening or ripening), and probably would be ready to spawn in midwinter. Chrzan and Zukowski (1966, in press) reported that the large argentines examined from the Scotian Shelf region in early July were mainly in stage VIII (resting). All these data suggest a late winter or early spring spawning in waters of the Scotian Shelf.

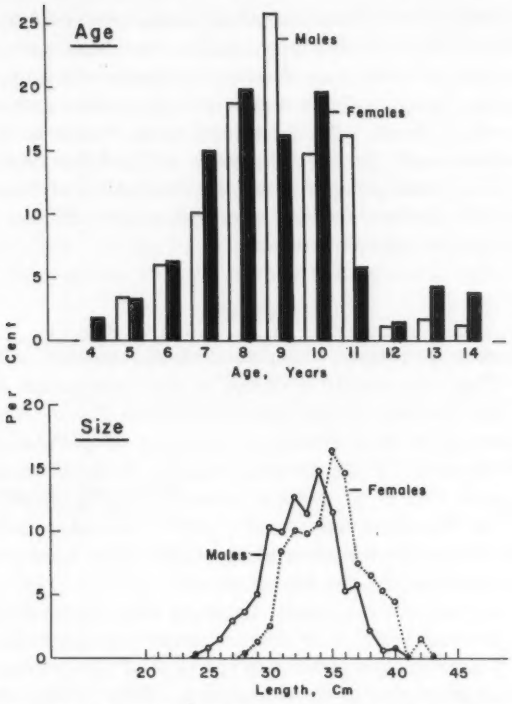

FIG. 10. Length and age of mature argentines from Emerald Basin in March 1965.

TABLE I. Development stages for mature argentines taken from Emerald Basin in March 1965.

Maturity stage	Males		Females	
	No.	*%*	*No.*	*%*
IV (ripening)	90	27.3	48	19.8
V (ripe)	234	71.2	149	60.5
VI (spawning)	5	1.5	45	18.5
VII (spent)	—	—	3	1.2
Total:	329		245	

FOOD AND FEEDING. From current studies there is little to add to previously published accounts about food of the argentine. Most of the feeding argentines examined contained crustaceans, either euphausiids or amphipods.

In March 1965, of 136 fish examined in the Emerald Basin region for stomach contents, 93% had empty stomachs. As noted previously, most of these fish were ripe or spawning. During September–October 1964 most of the fish taken in the Emerald Basin region were immature and of the stomachs examined from these about 70% contained food. South of Emerald Bank, again with immature and ripening fish, about 40% of the stomachs examined contained food. Our findings agree with the conclusion of Borodulina (1964) that adult argentines resume feeding after spawning and that feeding in fall would be more intensive than in winter.

DISCUSSION

Argentines are a deep-water form on both the eastern and western sides of the Atlantic. They are mainly confined to the continental slope, although they penetrate into the deep-water area of Emerald Basin. Why they do not penetrate into the Gulf of St. Lawrence is a matter of speculation. Our results suggest that the argentine in the western Atlantic is found mainly in warmer water (4–10 C) and this is in general agreement with observations in the eastern Atlantic by Kotthaus and Krefft (1957) and Borodulina (1964). It may be that the temperature regime in the Gulf of St. Lawrence is too cold for argentines, at least during the winter season.

Our results showed a relationship between size of argentines and depth of water on the Scotian Shelf, with smaller argentines generally occurring in shallower water. This is in agreement with the type of distribution of argentines reported from European waters by Borodulina (1964). They thus follow the pattern for many other species, such as redfish (Templeman, 1959), cod (Jean, 1964), and haddock (McCracken, 1966, in press). Our results also showed considerable segregation by size of fish in the area off central Nova Scotia. However, our data are insufficient to show whether or not this segregation is a stable relationship.

Recent papers by Borodulina (1964) and Chrzan and Zukowski (1966, in press) have described some characteristics of argentines from the Scotian Shelf. Borodulina (1964) has also compared information on morphometrics, age, growth, and maturity of argentines from both sides of the Atlantic. From some of the differences in morphometric characteristics, and particularly from differences in growth, Borodulina (1964) has suggested local populations off the North American coast. Our information on size differences within rather limited areas indicates some of the sampling problems involved in determining such relationships between stocks. However, our best catches of argentines have occurred in particular areas, and it may be that rather discrete local stocks exist; but in the areas covered in our surveys they do not show distinct differences in rate of growth.

It is interesting to compare our age and growth estimates for argentines with those of investigators from the USSR and Poland. Since these estimates are not from fish taken at precisely the same season, some adjustments to

facilitate comparison have been made (Tables II and III). Borodulina (1964) reports that most argentines in USSR samples had otoliths with narrow hyaline edges even though they were taken in August. He therefore rounded off ages to the nearest year (8+ = 9). Canadian samples taken in October have been treated in the same way since they would have completed most of the year's growth. Otoliths in Canadian samples taken in March had mainly hyaline edges and ages read from otoliths have not been adjusted. Polish samples taken in July would presumably be part way through the summer's growth and these have been shown in this manner in the tables. While the results obtained by the various investigators are in general agreement, there are

TABLE II. Comparison of length-at-age estimates for argentines from the Nova Scotian banks region by Canadian, Polish, and Soviet investigators. Numbers aged are shown in parentheses where known.

	Canadian		Polish		Soviet	
Age	Emerald–LaHave Bank October 1964 ♀ and ♂		Sable Island July 1964 ♀ and ♂		Sable Island (mainly August 1960)[a] ♀	♂
	cm		*cm*		*cm*	*cm*
1						
1+						
2	17.9	(59)				
2+						
3	20.9	(63)				
3+			20.2	(5)		
4	24.2	(64)				
4+			22.7	(12)		
5	26.8	(41)			27.8	26.0
5+			25.7	(9)		
6	28.9	(28)			28.8	27.5
6+			26.3	(10)		
7	30.8	(15)			30.0	28.5
7+			27.0	(15)		
8	32.4	(14)			30.7	29.8
8+			29.3	(9)		

[a]Probably a total of 100 fish. According to Borodulina (1964) Soviet age readings rounded off to even years, i.e. 5+ = 6; see text.

TABLE III. Comparison of length-at-age estimates for larger argentines from the Nova Scotian banks region by Canadian, Polish, and Soviet investigators. Numbers aged are shown in parentheses where known.

	Canadian				Polish		Soviet	
	Emerald Basin March 1965				Browns Bank[a] July 1964		LaHave Bank August 1960[b]	
Age	♀		♂		♀ and ♂		♀	♂
	cm		*cm*		*cm*		*cm*	*cm*
6	31.0	(7)	30.2	(5)			31.5	30.5
6+					30.7	(8)		
7	33.4	(8)	30.5	(11)			32.8	31.4
7+					31.1	(12)		
8	34.8	(15)	33.2	(14)			34.5	32.3
8+					32.2	(24)		
9	34.0	(21)	32.8	(13)			36.0	34.0
9+					32.5	(20)		
10	35.4	(11)	33.4	(14)			36.5	34.5
10+					32.8	(28)		
11	36.8	(12)	34.4	(6)			38.0	35.5
11+					33.8	(11)		
12							38.2	36.5

[a]Deep water.
[b]Ninety-nine fish in total. According to Borodulina (1964), Soviet age readings are rounded off to even years, i.e. 5+ = 6.

differences which occur either from variations in age-reading techniques or from actual differences in rate of growth for fish in different regions. However, all results show rapid growth in the first few years, with subsequent growth increments much reduced.

Argentines taken in the Emerald Basin region during March 1965 by Canadian investigators are the only fish taken in which gonads were approaching spawning condition. These results suggest that spawning takes place on the Scotian Shelf in March and April. Nothing is recorded in the literature about spawning time for this species on the North American side of the Atlantic. However, for the European side, Borodulina (1964) presents data to show that argentines spawn from April to July. In addition, Schmidt (1906) described the development of the eggs and larvae of *A. silus* which were taken bathypelagically from deep water of the northeast Atlantic between May and September.

In our winter catches, the smallest mature males and females were about 25 and 30 cm, respectively. A few mature fish were 4 and 5 years of age, but mature fish were not well represented in the catches until 6 or 7 years of age. Borodulina (1964) has described differences in rings in argentine otoliths similar to the spawning rings in cod otoliths (Rollefsen, 1933). He has attributed these to onset of maturation and from these rings he estimates ages of maturation for argentines. Of argentines from American waters, about 11% were maturing for the first time at 6 years of age, about 25% at 8 years of age, and all were mature by 10 years of age. Apparently argentines mature earlier on the North American side than on the European side of the Atlantic since estimations for the European side (Fridriksson, 1937) placed age at first maturity for argentines between 8 and 15 years. Borodulina (1964), using the spawning ring technique, estimated that about a third of argentines on the European side were still maturing for the first time at 10 years of age.

Our observation that feeding argentines contained mainly crustaceans, either euphausiids or amphipods, agrees with previously published accounts of their feeding habits. Both Cohen (1958) and Borodulina (1964) comment that the food composition of the argentine is quite uniform, both in North American and European waters, and consists mainly of *Sagitta* (arrow worms), Euphausiacea (krill), and *Themisto* (amphipods). Occasionally, squid, ctenophores, or fish remains were found in argentine stomachs.

Our observations indicate that a high proportion of mature argentines cease feeding at spawning time and agree with the conclusion of Borodulina (1964) that adult argentines resume feeding after spawning. His observations also suggest that feeding is more intensive in fall than in winter.

Since commercial landings of argentines from the North American area are a recent occurrence, some assessment of their potential seems useful. From 1963 to 1964, landings from Nova Scotia banks decreased markedly. Since argentines are a by-product of fishing for such species as silver hake, the changes in quantities of argentines landed probably do not reflect changes in abundance. However, it should be noted that in the North American region growth of argentines slows markedly after the second year and since they do not mature until 6–10 years of age, heavy fishing might reduce stocks and catches considerably below current levels. Borodulina (1964) has reached much the same conclusion. Our recent data on sizes and ages of argentines caught in the Emerald–LaHave Bank area during fall and winter 1964–65 compared with those of Borodulina (1964) taken in the summer of 1960 suggest that there may have already been considerable change in the size of fish in that area. In 1960, argentines were mainly large, between 30 and 40 cm; in 1964–65 they were mainly between 20 and 30 cm. Whether or not part of the difference may have resulted from seasonal changes in distribution is not yet resolved but the possibility of effects of fishing on this stock must be considered.

ACKNOWLEDGMENTS

The data presented in this paper were obtained through the efforts of a number of competent technicians in the groundfish investigation and with the aid of the crews of the research vessels *A. T. Cameron* and *Harengus* and chartered vessel *Alder Point*. A number of scientists in the groundfish investigation at the St. Andrews Biological Station aided by supervising cruises on which data were collected. It is a pleasure to acknowledge their assistance. The support and encouragement of Drs J. L. Hart and J. C. Medcof during the course of this work are much appreciated. The authors would also like to thank Drs A. C. Kohler, R. L. Saunders, and Mr A. Weinsieder for reading the manuscript and making constructive suggestions.

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Distributions and Comparisons of *Centrolophus niger* (Gmelin) and *Centrolophus britannicus* Günther (Centrolophidae) from the North Atlantic[1,2]

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ABSTRACT

The general distribution of *Centrolophus niger* in the North Atlantic is reviewed including the first two records from the Canadian area and two additional records off the New England coast to add to the four previously recorded from this area. Two new records from the Dana collections extend the distribution of this species westward in the oceanic area between Iceland and the Azores. All known records of the rarely captured *Centrolophus britannicus* are presented. These include 34 previously published records from the northeastern Atlantic, eight new records from the northeastern Atlantic and the first seven records from the northwestern Atlantic, from Flemish Cap and the southern Grand Bank to North Carolina.

In separating *C. niger* and *C. britannicus* some meristic characters are useful: *C. niger*, D. 35–41, A. 23–25, P. 20–23, gill-rakers on lower limb 1st arch, 13–15; *C. britannicus*, D. 44–51 (one, 55), A. 27–33 (one, 25), P. 18–21 (one, 16), gill-rakers on lower limb 1st arch, 11–13. Some body proportions are also important: the bases of the dorsal and anal fins are longer in *C. britannicus* and the distance from the snout to the anterior base of the dorsal fin usually greater. The length of the caudal peduncle is distinctly greater in *C. niger*.

In *C. niger* the flesh is firm and the skin tough whereas in *C. britannicus* the flesh is flabby and the skin delicate. The peritoneum of *C. britannicus* is usually dark and that of *C. niger* usually light.

INTRODUCTION

The black ruff, *Centrolophus niger* (Gmelin), has not previously been recorded from the Canadian area and only eight individuals (four in addition to our four new records) are known from the northwestern Atlantic. Its relative, *Centrolophus britannicus* Günther, has not previously been recorded from the northwestern Atlantic and only 34 have been recorded from the northeastern Atlantic. Our two specimens of *C. niger* are the first from the Canadian area and our seven specimens of *C. britannicus* are the first records from the Atlantic west and south of East Greenland.

[1]Received for publication February 23, 1966.
[2]Contribution No. 1774 from the Woods Hole Oceanographic Institution.

J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

A recent revision of the stromateoid fishes by Haedrich (MS, 1965), based largely on osteology, shows that *C. niger* and *C. britannicus* belong in fact to two different genera. Nonetheless, these two fishes externally resemble each other very much, and are often confused. The differences, especially in body proportions, between the two species are ill-defined. Examination of our specimens adds to the store of available information, and provides comparisons to render decisions on identification easier and more definite. For the present purpose, we prefer to use the more familiar names, and hence to treat the two fishes as though congeneric.

Except where otherwise noted, body measurements were taken by the standard methods of Hubbs and Lagler (1958). Apart from total lengths and standard lengths, which are shortest distances between parallel perpendicular planes, all measurements are direct distances between points.

DISTRIBUTION

Centrolophus niger (Gmelin) 1788 — Black ruff, blackfish

Centrolophus niger (Gmelin) 1788 (= *C. pompilus* Risso 1810) (Fig. 1) is a pelagic fish most common in the warmer parts of the North Atlantic (Fig. 2). It is broadly distributed in the northeastern Atlantic, ranging from Madeira (Fowler, 1936) to Norway (Collett, 1897; Grieg, 1911; Nordgård, 1931; Schaaning, 1940). In the Mediterranean it occurs as far east as the Adriatic (Sŏljan, 1948). Le Gall (1937), citing most of the important pretwentieth-century reports of this species, summarizes the approximate range as "Méditerranée, Atlantique: Madère, Açores. Côtes d'Espagne et du Portugal. Golfe de Gascogne. Mer Celtique. Entrée occidentale de la Manche. Côtes de Norvège. Côte orientale des États Unis."

Although essentially an oceanic fish, *C. niger* not infrequently wanders into the North Sea. From this area there are two recent records (Kotthaus, 1958; Roy, 1962). For Denmark, Jensen (1940) notes three and Nielsen (1963) an additional eight specimens, 48–58 cm long. Nybelin (1941) reports a specimen from Hunnebostrands harbour in Sweden, and Mathiasson (1965) two specimens from Sweden, one taken in the Skagerrack and the other in the southern Baltic 10 nautical miles south of Ystad.

Day (1880) reviewed the distribution of this species and recorded the captures in England and Ireland, and Jenkins (1925) noted additional records from England, Scotland, and Ireland.

In recent years at least 12 *C. niger* have been recorded from Scottish waters (Rae and Wilson, 1954, 1956; Rae and Lamont, 1960, 1961a, b, 1963, 1964) including one of 855 mm (Rae and Lamont, 1961b). Sir Frederick S. Russell (personal communication, November 13, 1964) has given us two English records of *C. niger* from the Plymouth Laboratory, one caught off Eddystone in August 1962 and the other stranded in the Scilly Isles in August 1964.

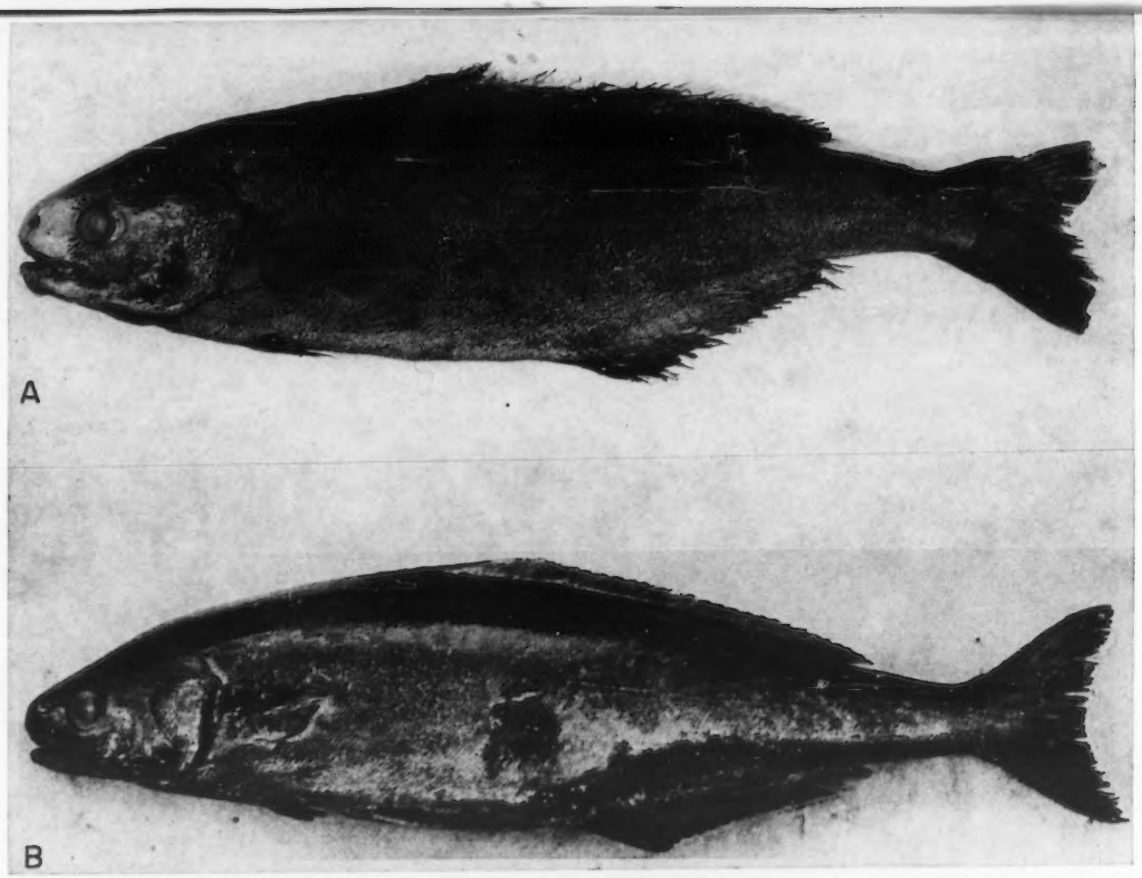

FIG. 1. *Centrolophus niger*: A, fork length 485 mm, from SE Grand Bank (Table I, No. 7): B, total length 1195 mm, female mature, from E of Georges Bank (Table I, No. 8).

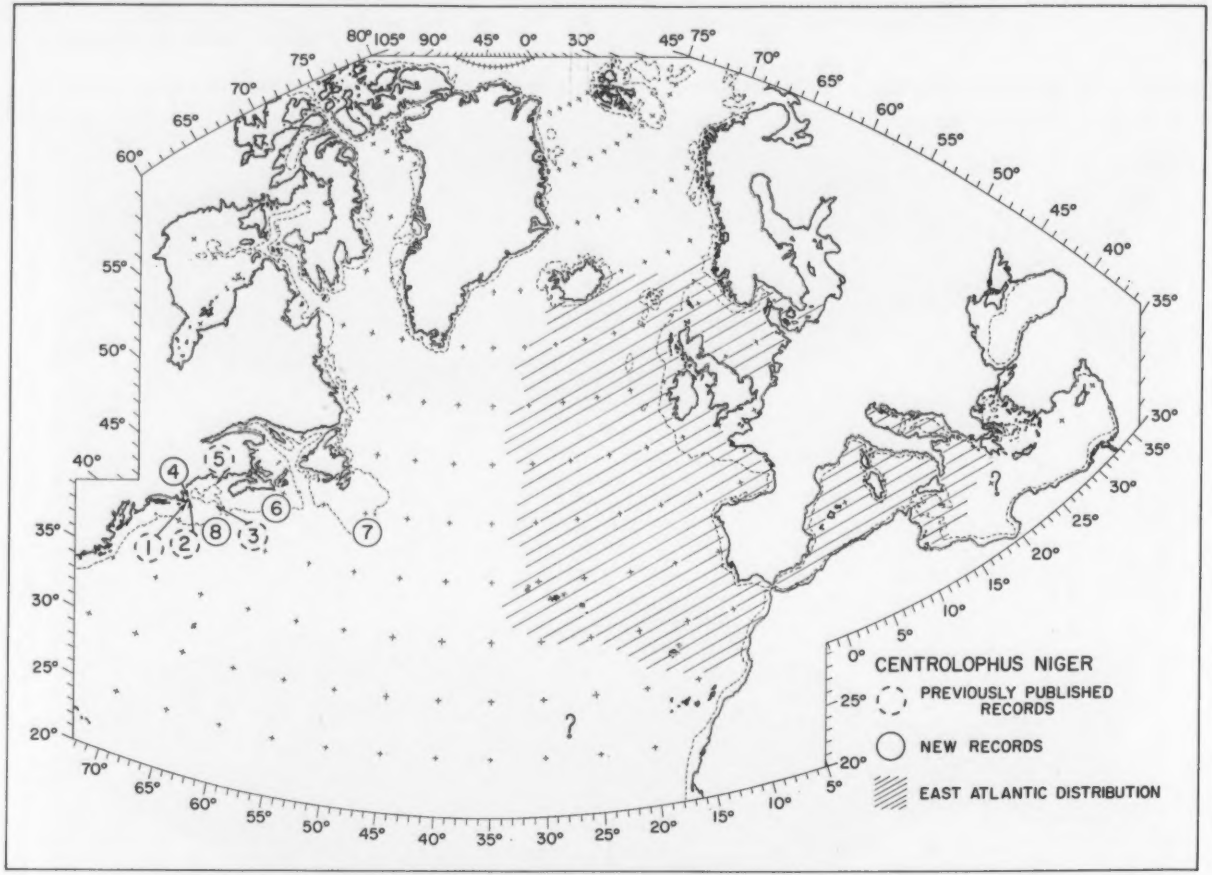

FIG. 2. North Atlantic distribution of *Centrolophus niger* including all known records from the western Atlantic and an outline of distribution in the eastern Atlantic. (Numbers refer to the specimens of Table I. The maps used for Fig. 2 and 5 were adapted from an outline chart of the North Atlantic Ocean on an azimuthal equal area projection centred at 40°N, 35°W, prepared at the Woods Hole Oceanographic Institution by M. I. Pollak and G. G. Pasley, April 1951).

outline chart of the North Atlantic Ocean on an azimuthal equal area projection centred at 40°N, 35°W, prepared at the Woods Hole Oceanographic Institution by M. L. Pollak and G. G. Pasley, April 1951).

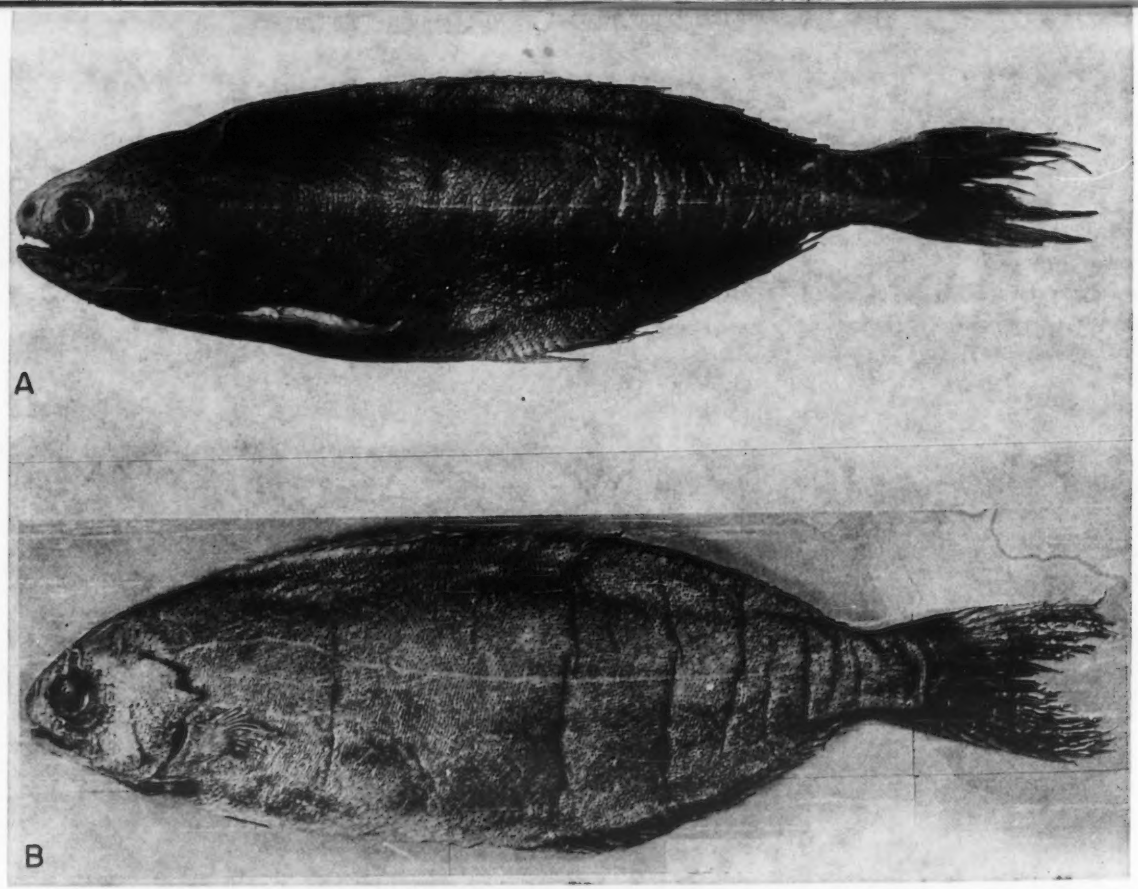

FIG. 3. *Centrolophus britannicus*: A, fork length 350 mm, female immature, from SW Grand Bank (Table II, No. 37); B, total length 525 mm, female mature, from SE Grand Bank (Table II, No. 32).

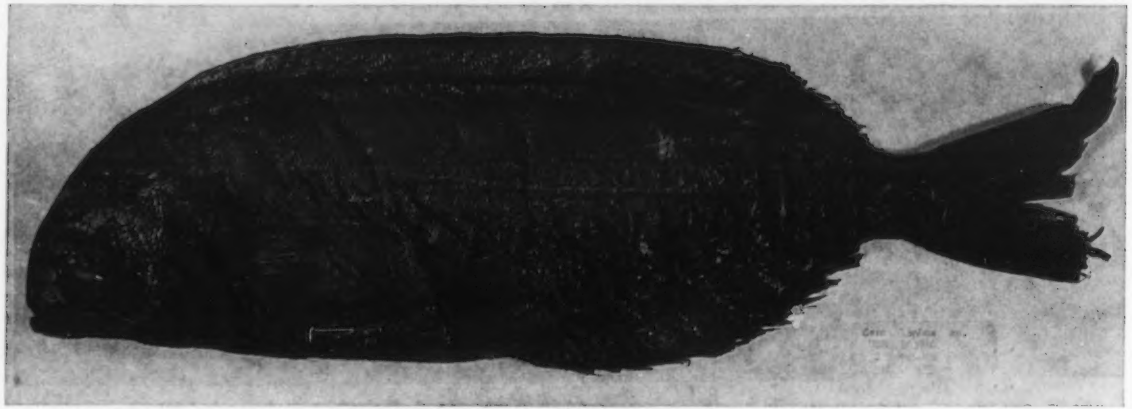

FIG. 4. *Centrolophus britannicus* with head bent ventrally and presumably naturally deformed in this respect: standard length 333 mm, male barely mature, from Kitty Hawk, North Carolina (Table II, No. 31).

Fraser-Brunner (1935) took 10 specimens of *C. niger*, two males and eight females, during a trawler cruise in July 1934 on the continental slope area, between 180–550 m deep, southwest of Ireland. Recent exploratory surveys of the Atlantic slope fishing grounds west of Ireland and Scotland show *C. niger* to be fairly common in the "Farm" area west of Ireland (Blacker, 1962). In the same survey, two fish were caught at Rockall Bank and over 1 cwt were offered but were not sold on the Milford Haven Market from one trip of the trawler *Boston Heron*. Small *C. niger* were commonly found in hake stomachs.

Two small *C. niger* from the Dana collection, taken at 51°48′N, 30°30′W, were recently examined by the second author (Table III, items 16, 17; Table IV). These records extend the westward range of this species in the area between Iceland and the Azores.

For Iceland, Saemundsson (1927, 1949) records the possibility of two fish from the southeast coast. These records, received in a personal communication from Dr A. Bowman, are perhaps doubtful as they were half digested and the fin rays could not be counted. Nonetheless, they agreed with *C. niger* in general appearance. Rae and Wilson (1952a, b), Brandes et al. (1953, 1956), Brandes and Kotthaus (1958, 1959, 1960), and Rae and Lamont (1964) record seven *C. niger* from the west to southeast coasts of Iceland, and one from the Iceland–Faroe Ridge ("Rosengarten"). One of these fish (Brandes and Kotthaus, 1959) was 1105 mm long.

There are apparently no records from Greenland (Dr Paul Hansen, personal communication, October 9, 1964) nor previously from the Canadian area. Hitherto from the northwestern Atlantic there are four records of *C. niger*, all from the east coast of the United States (Goode and Bean, 1896; Bean, 1898; Bigelow and Schroeder, 1937; Scattergood and Coffin, 1953).

Four new northwestern Atlantic records are presented, two from the United States area within the known range of the species. New records from Sable Island Bank and from the southeastern Grand Bank extend the range of this species northward and eastward in the western Atlantic (Fig. 2, Table I). The specimen from east of Georges Bank, obtained on December 5–6, 1963, was a spent female 1195 mm in total length.

Centrolophus britannicus Günther 1860 Cornish blackfish

This (Fig. 3, 4) is a rarely caught species for which the 34 previously published records (Fig. 5, Table II) range from East Greenland to the northeastern Atlantic. Our seven records, four from the southwestern slope and one from the southeastern slope of the Grand Bank, one from east of Flemish Cap and one from North Carolina, are apparently the first from the northwestern Atlantic. In addition three new records are noted from the eastern Atlantic. In the Northeast Atlantic, which seems to be the area of greatest abundance for both species, *C. britannicus* appears to be more northerly in distribution than *C. niger*.

TABLE I. Records of *Centrolophus niger* (Gmelin) from the western Atlantic. (T.L. = total length. S.L. = standard length. * = new records.)

Specimen No.	Reference	Locality and date of capture, etc.
1.	Goode and Bean (1896) U.S.N.M. 44440	Off Dennis, Mass., November 23, 1888, 23 cm T.L.
2.	Bean (1898) U.S.N.M. 48906	North Truro, Mass., September 6, 1930, 32 cm T.L. Offshore fish trap.
3.	Bigelow and Schroeder (1937) M.C.Z. 34246	N edge Georges Bank (42°10'N, 66°45'W), September 12, 1936, 528 mm T.L. Otter trawl, 238 m.
*4.	Authors (Haedrich) M.C.Z. 37983	Provincetown, Mass., June 23, 1951, 349 mm T.L. Fish trap.
5.	Scattergood and Coffin (1953)	Near Mount Desert Rock, Maine, October 12, 1951, 493 mm T.L. Otter trawl, 137–146 m.
*6.	Authors (Haedrich) M.C.Z. 37984	Sable Island Bank, September 25, 1953, 349 mm T.L. Otter trawl, 62 m.
*7.	Authors (Templeman)	SE slope of Grand Bank, probably between 43° and 44°N and 49°10' and 49°00'W, August 5–11, 1959, 445 mm S.L. Otter trawler *Zebu*, ca. 330 m.
*8.	Authors (Haedrich)	E of Georges Bank, 40°13'N, 65°45'W, December 5–6, 1963, 1195 mm T.L. Female mature, recently spent. *Delaware*, floating longline.

BODY PROPORTIONS AND OTHER CHARACTERISTICS

For both *C. niger* and *C. britannicus* adequate measurements for comparison within and between the species are only rarely presented. Where measurements and comparisons are given they are often in terms of the total length with no provision of a standard length. Total length is unsatisfactory in that it may be measured in a number of ways and the tips of the fins are often broken off. There is, as a rule, no statement on which of the three or more possible total lengths were used. Data on meristic characters are more adequate but often not completely convincing because of a lack of description of the method of finding and counting the anteriormost dorsal and anal fin elements. These elements, at least in preserved specimens, are tightly attached along the fin border and although visible externally need dissection to be clearly seen. With growth, more and more may become bound.

We have, therefore, given (Tables III–V) a number of standard meristic data and body proportions, both to compare with available data of a similar kind and to provide future investigators with a working base for comparison.

INTRASPECIFIC COMPARISONS

For both *C. niger* and *C. britannicus* (Tables III–V), our northwestern Atlantic specimens usually come within the range of other individuals of

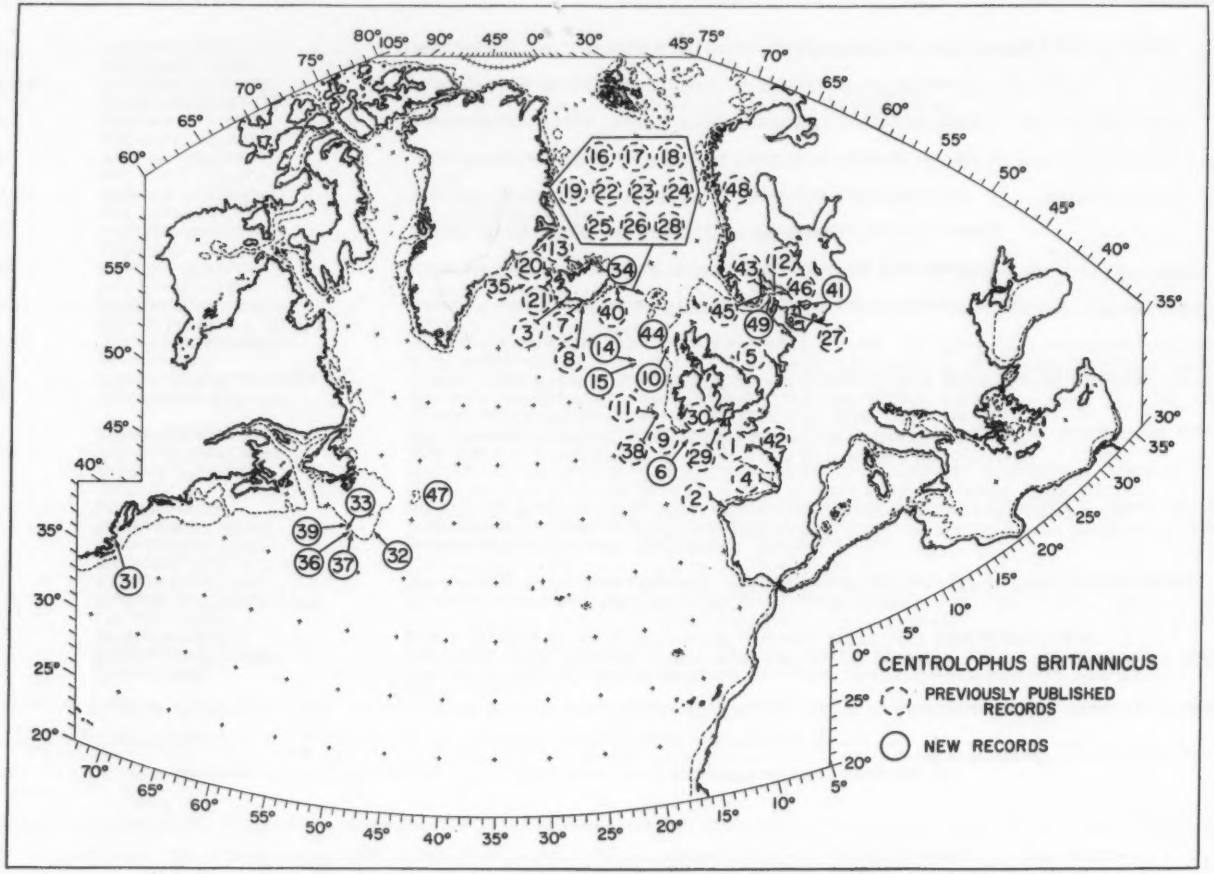

FIG. 5. Distribution of *Centrolophus britannicus*, including all records known to the authors. (Numbers refer to the specimens of Table II.)

TABLE II. Records of *Centrolophus britannicus* Günther. (T.L. = total length. S.L. = standard length. * = new records.)

Specimen No.	Reference	Locality and date of capture, etc.
1.	Gunther (1860a,b)	Polperro (close to Looe), Cornwall, England, February 1859, 483 mm T.L. Holotype. Washed ashore after storm.
2.	Cligny (1905)	Close to La Coruña, Northwest Spain, December 1904, 511 mm T.L. Trawl, 275–320 m.
3.	Saemundsson (1908)	Grindavik, Iceland, March 7, 1905, 445 mm[a], male.
4.	Pellegrin (1912) Dubalen (1930)	Capbreton, Bay of Biscay, France, March 1908. By hand at surface after storm.
5.	Duncker and Mohr (1929)	Onrust, a small island near Texel, Holland, April 27, 1912.
* 6.	Authors (Haedrich) B.M.N.H. 1916.8.3.2	NE Atlantic, 95 nautical miles SSE Bull Rock (SW Ireland), 550 m, 1916, large specimen.
7.	Saemundsson (1922)	Vestmannøhavn, Iceland, April 8, 1921, 520 mm, male.
8.	Saemundsson (1927)	Vestmannøhavn, Iceland, October 6, 1922, 232 mm.
9.	Le Gall (1925)	Grande Sole Bank, W. entrance, English Channel, March 10, 1925, 388 mm T.L. Trawl, 160–200 m.
*10.	Authors (Haedrich) B.M.N.H. 1929.4.17.1	NE Atlantic, 70 nautical miles NW Barra Head (Outer Hebrides, W Scotland), > 490 m, 1929, large specimen.
11.	Fraser-Brunner (1935)	SW of Ireland, 52°35′N, 13°03′W, 503 m, July 1934, 380 mm S.L., male. British Otter trawler *Dynevor Castle*. (Checked by authors (Haedrich) B.M.N.H. 1934.8.8.75.)
12.	Gustafson (1939)	Bohuslan, Sweden, October 1939, 60 cm. Trawl, 287 m.
13.	Nielsen (1963) and letter January 1964	Twenty miles NNW of Sandanesi [presumably Saudanes] N coast Iceland, September 2, 1947. *M.B. Bligandi*.
*14–15.	Authors (Haedrich) B.M.N.H. 1950.7.20.1–12	NE Atlantic, Rockall, 1950, large specimens.
16–17.	Brandes, Kotthaus and Krefft (1953)	Iceland–Faroe Ridge, September 22, 1948. Presumably by otter trawler.
18.	Brandes, Kotthaus and Krefft (1953)	Iceland–Faroe Ridge, August 8, 1950. Presumably by otter trawler.
19.	Brandes, Kotthaus and Krefft (1953)	Iceland–Faroe Ridge, August 28, 1950. Presumably by otter trawler.
20–21.	Brandes, Kotthaus and Krefft (1953)	Víkuráll, Iceland, June 18, 1951. Presumably by otter trawler.
22.	Brandes, Kotthaus and Krefft (1953)	Iceland–Faroe Ridge, July 13, 1951. Presumably by otter trawler.
23.	Brandes, Kotthaus and Krefft (1953)	Iceland–Faroe Ridge, July 16, 1951, Presumably by otter trawler.
24–26.	Brandes, Kotthaus and Krefft (1953)	Iceland–Faroe Ridge, July 22, 1951. Presumably by otter trawler.
27.	Nielsen (1963)	Kalundborg Fjord, Denmark, September 6, 1952, 475 mm T.L. Herring trawl, 15–20 m.

28.	Brandes, Kotthaus and Krefft (1953)	Iceland–Faroe Ridge, November 14, 1952. Presumably by otter trawler.
29.	G. A. Steven (1955)	W shore of Bryher, Isles of Scilly, Cornwall, England, June 1, 1954. Set Net.
30.	G. A. Steven (1955)	Westward Ho, Devon, England, June 3, 1954. Washed ashore.
*31.	Authors (Haedrich) U.S.N.M. 163880	Kitty Hawk, North Carolina, U.S.A., September 1954, 333 mm S.L., male barely mature.
*32.	Authors (Haedrich)	SE slope Grand Bank, February 20, 1958, 525 mm T.L., female mature. U.S.A. Otter trawler *Storm*.
*33.	Authors (Templeman)	SW slope Grand Bank, May 24–28, 1958, 275–310 m, 306 mm S.L., female immature. Nfld. Otter trawler *Gaultois*.
*34.	Authors (Haedrich) B.M.N.H. 1958.9.30.1	E Iceland, 330 m, ca. 450 mm S.L., female, 1958.
35.	Krefft (1960)	East Greenland, 65°27′N, 30°05′W, October 3, 1958, 420–430 m, 388 mm S.L. First record for Greenland waters.
*36.	Authors (Templeman)	SW slope Grand Bank between 52°05′W and 52°45′W, April 1959, 318 mm S.L., female immature. Nfld. Otter trawler *Pennyluck*.
*37.	Authors (Templeman)	SW slope Grand Bank, 43°16′N, 51°38′W, May 5, 1959, 333–358 m, bottom temperature 3.10 C, 315 mm S.L., female immature. *A. T. Cameron*, otter trawl, V. M. Hodder, Scientist-in-charge.
38.	Blacker (1962)	"Farm" W of Ireland, S of Porcupine Bank, July 8–9, 1960, 56 cm. *Ernest Holt*, otter trawl.
*39.	Authors (Templeman)	SW slope Grand Bank, 44°00′N, 52°30′W, February 4, 1961, 200–220 m, 32 cm S.L. Nfld. Otter trawler *Blue Mist II*.
40.	Krefft (1964)	Western edge of Iceland–Faroe Ridge, July 2, 1962, 480 m, 58 cm T.L.
*41.	Jørgen Nielsen, letter January 9, 1964	NW Zealand (Sjaellands Odde), 56°N, 11°15′E, summer 1962, 40 cm.
42.[b]	Amanieu and Cazaux (1963)	Arcachon, France, March 30 or September 29, 1963, in shallow water, 50 cm T.L.
43.	Nybelin (1964)	N of Hirtshals, Denmark, January 23, 1963, 451 m, ca. 575 mm T.L. Shrimp trawl.
*44.	Dr G. Krefft, letter May 17, 1965	Rosemary Bank E, 59°07′N, 10°03′W, January 22, 1964, 630–640 m, bottom temperature 8.8 C, 40 cm T.L. *Anton Dohrn*, otter trawl.
45.	Nybelin (1964)	NW of Skagen, Denmark, January 31, 1964, 55 cm T.L.
46.	Mathiasson (1965)	Between Måseskär (near Göteborg) Sweden and Skagen, Denmark, June 25, 1964, 94–113 m.
*47.	Authors (Haedrich)	W Atlantic E of Flemish Cap, 47°11′N, 42°11′W, September 12, 1964, 0–35 m, 320 mm T.L., male immature. *Atlantis II*, 10-ft Isaacs Kidd midwater trawl.
48.	Borgstrøm (1965)	Region of Rana in Nordland province, Norway, January 22, 1965, 430 mm T.L.
*49.	Jørgen Nielsen, letter April 27, 1965	20 nautical miles NW of Hirtshals, northern Jutland, Denmark, February 4, 1965, 60 m, length 600 mm, weight 2 k. Bottom trawl.

[a]Forty-six cm in Saemundsson (1908) but 445 mm with body proportions in Saemundsson (1913).
[b]Reported as *C. niger* but *C. britannicus* from figure, anal fin-rays and body proportions. These authors also report a second specimen of *C. niger* from the same locality. This specimen may also be *C. britannicus* but is not included here.

TABLE III. Meristic and other number characteristics in *Centrolophus niger* and *C. britannicus*.

Item No.	Location of capture	Date of capture	Reference	Total length, *mm*	Total length to mid-fork, *mm*	Standard length, *mm*	Dorsal fin rays, No.	Anal fin rays, No.	Pectoral fin rays, No.	Pelvic fin rays, No.	Scales in lateral line, No.	Caudal (principal) rays, No.	Vertebrae, No.	Pyloric caeca, No.	Branchiostegal rays, No.	Gill rakers, anterior arch, No.
							C. niger									
1.	Summary of the whole range of knowledge, not applying to individual specimens, from: Cuvier and Valenciennes, 1833; Günther, 1860b; Goode and Bean, 1896; Regan, 1902; Le Gall, 1937.			...	...	...	37–41	23–25	21	6	160–205, $\frac{23–28}{58–70}$	17	25	9–10	7	...
2.	?	?	Cuvier and Valenciennes (1833)	...	...	...	39,41	23	21	6	...	17	...	...	7	...
3.	Byneset, Trondheim Fjord	September 8, 1886	Collett (1897) Specimen (a)	425	...	...	41	25	21	6	...	...	...	...	...	...
4.	Byneset, Trondheim Fjord	September 8, 1886	Collett (1897) Specimen (b)	449	...	...	37[a]	24	21	6	...	...	...	...	...	...
5.	West of Florès, Azores	1887	Collett (1896)	212	...	...	38	24	21	...	...	...	...	...	...	...
6.	Dennis, Mass.	November 23, 1888	Authors (Haedrich)	223	...	189	40[b]	23[b]	21	...	...	...	25[c,d]	...	...	6+15[e]
7.	North Truro, Mass.	September 6, 1890	Authors (Haedrich)	324	...	265	38[b]	24[b]	20	...	...	...	25[c,d]	...	...	5+15[e]

8.	Hegrenes, Bergen Fjord	February 23, 1904	Greig (1911)	670	...	...	35	25	22	6	...	17	...	...	...	...
9.	La Coruña, NW Spain	November 1904	Cligny (1905)	<519[f]	...	...	40	25	21	6	ca. 160	...	...	...	...	...
10.	Western entrance to English Channel	...	Cligny (1905)	519	...	...	40	23	...	...	...	...	...	...	...	..
11.	Blokhus, Denmark	April 24, 1919	Jensen (1921)	...	400	...	39	25[g]	21	6	...	...	...	...	...	...
12.	Mediterranean	...	Jensen (1921)	...	...	...	41	24	...	...	...	...	...	...	...	...
13.	Mediterranean	...	Jensen (1921)	...	...	...	40	25	...	...	...	...	...	...	...	...
14.	Mediterranean	...	Jensen (1921)	...	...	...	37	23	...	...	...	...	...	...	...	...
15.	Villefranche-sur-Mer, France	May 3, 1930	Chabanaud and Trégouboff (1930)	...	...	188	ca. 38	ca. 25	20	6	...	...	...	...	7	4+13
16.	Dana sta. 4205 VI, 51°48′N, 30°30′W In 2-m stramin net with 50 m wire out	July 1, 1931 0045 hr	Authors (Haedrich)	188	...	147	39[b]	24[b]	22	...	...	...	25[c]	...	...	5+14[e]
17.	Dana sta. 4205 VI, 51°48′N, 30°30′W In 2-m stramin net with 50 m wire out	July 1, 1931 0045 hr	Authors (Haedrich)	255	...	204	37[b]	24[b]	22	...	...	...	25[c]	...	...	5+14[e]
18.	Georges Bank	September 12, 1936	Bigelow and Schroeder (1937)	...	...	469	38	25	21	...	ca. 185	...	...	...	...	5+13
19.	Provincetown, Mass.	June 23, 1951	Authors (Haedrich)	349	...	284	38[b]	24[b]	21	...	ca. 210	...	...	...	...	5+13[e]
20.	Maine	October 12, 1951	Scattergood and Coffin (1953)	493	454	410	37	24	22	6	205	...	...	...	...	...
21.	Sable Island Bank	September 25, 1953	Authors (Haedrich)	600	...	490	37[b]	25[b]	21	...	ca. 210	...	...	...	...	5+13[e]
22.	SE slope Grand Bank	August 5–11, 1959	Authors (Templeman)	...	485	445	41[b]	23[b]	23	6	...	17[h]	25[c]	...	...	6+15[e]
23.	E of Georges Bank	December 5–6, 1963	Authors (Haedrich)	1195	...	1065	38[b]	24[b]	22	...	ca. 165	...	...	...	...	5+14[e]

(*Continued*)

TABLE III. Meristic and other number characteristics in *Centrolophus niger* and *Centrolophus britannicus*. — (*Concluded*)

Item No.	Location of capture	Date of capture	Reference	Total length, *mm*	Total length to mid-fork, *mm*	Standard length, *mm*	Dorsal fin rays, No.	Anal fin rays, No.	Pectoral fin rays, No.	Pelvic fin rays, No.	Scales in lateral line, No.	Caudal (principal) rays, No.	Vertebrae, No.	Pyloric caeca, No.	Branchiostegal rays, No.	Gill rakers, anterior arch, No.
							C. britannicus (see Table II)									
1.	Cornwall, England	February 1859	Günther (1860b)	483	...	...	45	30	...	...	...	...	...	...	7	...
			Day (1880)	...	...	...	46	30	...	6	...	17	...	...	7	...
			Authors (Haedrich)	460	...	ca. 405	46[b]	30[b]	18	...	ca. 230	...	...	...	...	...
2.	La Coruña, NW Spain	December 1904	Cligny (1905)	511	...	...	46	28	21	6	...	17	...	...	...	...
3.	Grindavik, Iceland	March 7, 1905	Saemundsson (1913)	445	...	...	46	25	21	6	...	16	...	9	7	5+12
4.	Capbreton, Bay of Biscay, France	March 1908	Pellegrin (1912)	501	...	...	49	33	20	6	ca. 190	17	...	...	...	...
5.	Vestmannøhavn, Iceland	April 8, 1921	Saemundsson (1922)	520	...	...	47	31	21	6	...	21	...	...	...	...
6.	Vestmannøhavn, Iceland	October 6, 1922	Saemundsson (1927)	232	...	...	51	31	21	7	...	17[i]	...	...	...	...
7.	Grand Sole Bank, W entrance English Channel	March 10, 1925	Le Gall (1925)	388	...	335	47	27	16	6	...	4+14+4	...	...	7	...
8.	Bohuslan, Sweden	October 1939	Gustafson (1939)	600	...	...	46	29	...	...	...	...	...	...	...	...
9.	Kalundborg Fjord, Denmark	September 6, 1952	Nielsen (1963)	475	...	395	55[j]	31[j]	19	6	178	16[k]	25[e,j]	...	...	6+11
10.	Kitty Hawk, North Carolina, U.S.A.	September 1954	Authors (Haedrich)	...	...	333	44[b,j]	28[b,j]	20	...	190	...	25[e,d]	...	...	5+12[e]

11.	SE Grand Bank	February 20, 1958	Authors (Haedrich)	525	...	435	44[b]	28[h]	18	...	ca. 180	...	...	...	...	5+12[e]
12.	SW slope Grand Bank	May 24–28, 1958	Authors (Templeman)	...	347	306	48[b]	30[b]	20	6	...	17[h]	25[e]	...	7	6+12[e]
13.	SW slope Grand Bank	April 1959	Authors (Templeman)	...	356	318	46[b]	29[b]	21	7	...	17[h]	25[e]	...	8	7+12[e]
14.	SW slope Grand Bank	May 5, 1959	Authors (Templeman)	...	350	315	50[b]	29[b]	21	6	...	17[h]	25[e]	9[m]	7	5+13[e]
15.	Arcachon, France	March 30, or September 29, 1963	Amanieu and Cazaux (1963)[n]	500	455[o]	406[o]	41[p]	30	20	6	...	...	...	...	...	...
16.	NW of Skagen	January 31, 1964	Nybelin, 1964	550	...	465	46	30	19	...	...	...	...	...	...	...
17.	NW Atlantic, E of Flemish Cap	September 12, 1964	Authors (Haedrich)	320	...	258	47[b]	30[b]	20	...	...	...	...	...	...	5+12[e]
18.	Region of Rana in Nordland province, Norway	January 22, 1965	Borgstrøm (1965)	430	...	...	48	27	...	...	...	...	...	...	...	...

[a]Corrected from 47 in Collett's publication. See text for explanation.
[b]Fin-ray bases. Rays visible without dissection but anteriorly not distinct before dissection. The last ray is bifid to the base but counted as one.
[c]Including urostylar half-vertebra as 1 vertebra.
[d]Pre-caudal 10, caudal 15.
[e]Including 1 gill raker in angle with number on lower limb. (Lower limb best for comparison since upper limb count includes a number of stubs, some of which may be missed, whereas rakers of lower limb are readily seen.)
[f]A little less than 519 mm.
[g]The last ray of the fin is double but was counted as 1.
[h]Branched rays +2. In each case 8 branched rays above and 7 below.
[i]Complete rays.
[j]Using X-rays.
[k]Articulated rays.
[l]Given as 24 by Nielsen but checked by Haedrich as 25 including the hypural (with the urostylar half-vertebra) as a vertebra.
[m]Main bases only, tips very much divided.
[n]*C. niger* in Amanieu and Cazaux (1963) but *C. britannicus* by figure, body proportions and number of anal rays.
[o]Calculated from photographic figure.
[p]This number is below the range of *C. britannicus*. It would be profitable to check the dorsal rays of this specimen as the most anterior rays are readily missed in counting.

TABLE IV. Body proportions of *Centrolophus niger*. (Except when noted otherwise all percentages are of the standard length.)

Item	Body part	Authors (Haedrich) Table III, *C. niger*, No. 16	Authors (Haedrich) Table I, No. 1	Authors (Haedrich) Table III, *C. niger*, No. 17	Authors (Haedrich) Table I, No. 2	Authors (Haedrich) Table I, No. 4	Collett (1897)	Collett (1897)	Scattergood & Coffin (1953) Table I, No. 5	Cligny (1905)	Authors (Templeman) Table I, No. 7	Bigelow & Schroeder (1937) Table I, No. 3	Authors (Haedrich) Table I, No. 3	Authors (Haedrich) Table I, No. 6	Grieg (1911)	Authors (Haedrich) Table I, No. 8
1.	Total length, *mm*	188	223	255	324	349	425[a]	449[b]	493	519	[c]	528[d]	ca. 540	600	670	1195
2.	Total length: to mid-fork, *mm*	...	...	...	...	...	393	412	454	...	485	...	...	...	628	...
3.	Standard length: snout to end hypural or base caudal, *mm*	147	189	204	265	284	338[e]	354[e]	410	419	445	469	ca. 443	490	530	1065
4.	Head: length, %	29.3	24.9	27.0	24.5	23.6	23.7	23.7	20.0	24.5	23.1	20.9	...	22.7	25.5	22.3
5.	Eye: horizontal diameter, %	6.8[f]	5.8[f]	6.4[f]	4.9[f]	4.2[f]	5.6	5.4	3.9	5.2	4.8[f]	4.1	...	4.3[f]	4.7	4.2[f]
6.	Interorbital width, %	10.2[g]	7.9[g]	9.3[g]	7.5[g]	8.5[g]	...	...	...	8.6	8.1[g]	...	7.9[g]	7.1[g]	...	8.2[g]
7.	Snout: length, %	9.5[h]	6.9[h]	8.3[h]	6.8[h]	7.4[h]	5.9	6.2	...	6.8	6.4[h]	...	7.0[h]	6.9[h]	8.5	7.6[h]
7A.	Head: post-orbital length, %	...	...	...	...	...	11.8	12.1	...	12.8	...	...	...	...	12.3	...
8.	Upper jaw: premaxillary symphysis – post. end maxillary, %	10.2	9.5	9.3	8.7	8.1	...	...	7.1	...	8.1	7.7	...	8.0	...	8.3
8A.	Premaxillary symphysis – end maxillary, % length of head	34.2	38.3	34.5	35.4	34.3	...	...	35.4	...	35.0	36.7	...	35.1	...	37.0
9.	Longest gill-raker 1st arch: length, %	...	...	...	...	...	...	...	...	...	2.7	...	...	...	...	...
10.	Snout – beginning dorsal fin, %	36.7	33.3	34.3	35.8	33.1	28.4	30.5	...	28.4	29.5	...	32.5	32.0	24.2	32.8
11.	Snout – anus (mid-cloaca), %	...	...	...	...	48.6	53.8	55.9	...	53.5	51.4	...	...	...	52.5	50.1
11A.	Snout – beginning anal fin, %	57.1	55.0	56.9	51.7	50.4	...	...	...	...	...	...	55.1	56.3	...	55.5

12.	Height: greatest body, %	30.6	29.1	26.0	26.4	25.7	27.8	28.0	26.8	26.8	25.8	28.6	...	28.8	26.0	26.7
13.	Height: body at anus, %	...	...	...	...	...	...	...	...	...	25.1	...	...	...	...	...
14.	Height: least of caudal peduncle, %	9.5	9.0	7.4	7.9	7.4	8.9	8.8	...	7.7	8.4	...	8.8	8.4	8.1	7.3
15.	Post. end dorsal base – mid-base caudal, %	19.7	...	19.6	...	22.9	...	...	...	...	20.2	...	...	...	...	19.0
16.	Post. end anal base – mid-base caudal, %	18.4	...	18.6	...	20.8	...	...	...	...	18.0	...	...	...	...	18.3
17.	Greatest width (thickness): body, %	...	...	...	...	10.6	...	...	...	12.6	11.5[i]	...	...	...	...	12.2
18.	Greatest width (thickness): head, %	...	...	...	...	...	...	...	...	...	11.0	...	...	...	...	...
19.	Dorsal fin: length of base, %	56.5	57.7	52.9	53.1	54.2	59.8	57.3	...	59.2	53.8	...	...	55.7	48.7	55.4
20.	Anal fin: length of base, %	27.9	30.2	29.4	30.2	29.6	33.1	31.6	...	30.4	29.2	...	...	29.4	29.8	28.7
21.	Pectoral fin: length, %	19.7	17.5	16.2	15.1	15.8	14.2	13.6	...	...	13.9	...	13.3	13.9	11.1	10.0
22.	Pelvic fin: length, %	15.0	11.6	11.8	12.1	11.3	8.9	8.8	...	...	8.1	...	8.6	7.8	8.7	5.8
23.	Caudal fin: length, %	...	...	...	...	...	25.7	26.8	...	23.9	...	...	...	...	...	...
24.	Anal beginning below what ray of dorsal, No.	...	...	...	...	19	...	...	...	...	22	...	...	...	...	...
25.	Sex and maturity	...	...	...	...	...	...	...	...	...	...	...	...	...	...	F, mat., spent
26.	Condition when measured	Good, ex formalin	Ex alcohol	Good, ex formalin	Ex alcohol	Very good, ex alcohol	...	...	...	...	Good, ex formalin, in water 2 days	...	Ex alcohol	Very poor, ex alcohol, perhaps salted	...	Good, fresh frozen
27.	When measured	1965	1964	1965	1964	1964	...	...	...	...	September 17, 1964	...	1964	1964	...	1964

[a]Collett's specimen (a).
[b]Collett's specimen (b).
[c]Unsuitable for this measurement.
[d]Given as total length but probably total length to mid-fork.
[e]Total length less caudal length.
[f]Space in skin through which eye is visible.
[g]Least fleshy width.
[h]To anterior edge of skin bordering eye.
[i]Not at neck.

TABLE V. Body proportions of *Centrolophus britannicus*. (Except when noted otherwise all percentages are of the standard length.)

Item	Body part	Authors (Haedrich) Table II, No. 47	Authors (Templeman) Table II, No. 37	Authors (Templeman) Table II, No. 36	Authors (Haedrich) Table II, No. 31	Le Gall (1925) Table II, No. 9	Saemundsson (1913) Table II, No. 3	Nielsen (1963) Table II, No. 27	Amanieu and Cazaux (1963)	Cligny (1905) Table II, No. 2	Authors (Haedrich) Table II, No. 32
1.	Total length, *mm*	320	[a]	[a]	...	388	445	475	500	511	525
2.	Total length: to mid-fork, *mm*	...	350	356	...	...	...	...	455[b]	...	...
3.	Standard length: to end hypural or base caudal, *mm*	258	315	318	333	335	368[c]	395	406[b]	427[c]	435
4.	Head: length, %	21.7	20.6	21.7	22.2	20.3	21.7	21.7	22.7	20.1	22.8
5.	Eye: horizontal diameter, %	3.5[d]	4.3[e]/4.4[d]	4.2[e]/5.0[d]	5.4[d]	3.6/4.2[f]	4.9	4.1	4.9	4.1	6.0[d]
6.	Interorbital width, %	9.3[g]	7.9[g]	6.3[g]	8.1[g]	6.6	...	7.4	...	6.6	8.0[g]
7.	Snout: length, %	7.4[h]	6.0[h]	6.0[h]	6.3[h]	5.1	...	5.1	5.4	5.9	6.7[h]
7A.	Head: post-orbital length, %	...	...	...	...	11.0	...	...	...	11.1	...
8.	Upper jaw: premaxillary symphysis – post. end maxillary, %	8.1	8.3	8.8	8.4	...	6.8	...	...	...	8.7
8A.	Premaxillary symphysis – end maxillary, % length of head	37.5	40.0	40.6	37.9	...	31.3	...	...	...	38.4
9.	Longest gill-raker 1st arch: length, %	...	2.5	2.9	...	...	2.2	...	...	...	...
10.	Snout – beginning dorsal fin, %	24.4	20.6	23.9	29.7	23.0	...	...	24.6	22.7	29.4
11.	Snout – anus (mid-cloaca), %	48.8	49.8	49.7	46.5	50.4	46.2	...	...	52.1	51.3
11A.	Snout – beginning anal fin, %	50.4	...	...	52.9	...	...	...	53.0	...	56.3
12.	Height: greatest body, %	32.9	29.8	28.9	33.9	28.4	29.9	...	29.6	29.9	34.0
13.	Height: body at anus, %	...	29.8	28.9	...	...	...	38.1	...	...	...
14.	Height: least of caudal peduncle, %	7.8	7.6	7.9	9.0	6.9	6.0	9.4[i]	...	8.0	9.2
15.	Post. end dorsal base – mid-base caudal, %	15.1	[a]	14.3	15.0	...	...	...	...	...	14.7

16.	Post. end anal base – mid-base caudal, %	14.3	[a]	13.2	15.3	...	...	...	. .	...	13.8
17.	Greatest width (thickness): body, %	11.2	8.2[j]	5.7[j]	9.3	7.5[k]	...	...	...	6.3	11.0
18.	Greatest width (thickness): head, %	...	10.2	9.4	...	9.3	...	...	...	...	...
19.	Dorsal fin: length of base, %	66.3	67.9	70.8	71.5	64.2	63.9	...	69.0	65.8	69.0
20.	Anal fin: length of base, %	36.8	35.9	36.2	37.2	37.3	35.3	...	38.7	36.7	36.8
21.	Pectoral fin: length, %	9.7	12.1	12.6	13.2	11.6	8.2[l]	...	...	...	11.0
22.	Pelvic fin: length, %	7.4	6.3	6.6	7.8	5.7	4.9[l]	...	...	...	5.1
23.	Caudal fin: length, %	...	[a]	[a]	...	...	20.9	...	...	19.6	...
24.	Anal beginning below what ray of dorsal, No.	20	[a]	18	22	...	[19[m]]	...	...	...	21
25.	Sex and maturity	M, imm.	F, imm.	F, imm.	M, mat.	...	M	...	...	...	F, mat.
26.	Condition when measured	Good, ex alcohol, originally 3 months in formalin	Good, ex formalin and in water for 2 days		Good, ex alcohol[n]	...	...	...	...	...	Good, ex alcohol, originally 5 yr in formalin
27.	When measured	1965	September 18, 1964	September 18, 1964	1964	...	...	...	...	...	1964

[a]Unsuitable condition for this measurement.
[b]Calculated from photographic figure of Amanieu and Cazaux (1963). The specimen of Amanieu and Cazaux was reported as *C. niger* but has the appearance and characteristics of *C. britannicus*.
[c]Calculated by subtracting length of caudal from total length.
[d]Space in skin through which eye is visible.
[e]Cornea only.
[f] Diameter orbit.
[g]Least fleshy width.
[h]To anterior edge of skin bordering eye.
[i] Calculated from Nielsen's photograph of *C. britannicus*.
[j] Not at neck.
[k]At level of pectorals.
[l] Longest fin-rays only.
[m]From Günther (1860b) for the holotype from Cornwall.
[n]In this specimen the head was deformed, the snout and mouth extending further ventrally than usual. This has the effect of increasing dorsal distances and reducing ventral distances measured from the snout (Fig. 4).

the same species in body proportions and in meristic characters. With occasional specimens there is an extension to the meristic or body-proportion range.

Interspecific Comparisons

Meristic characteristics (table III)

In the following discussion of fin-ray numbers we shall not differentiate between fin rays and spines. This distinction is observed by some authors, but the weakly-developed spines are separated from the rays only with difficulty. It is much more convenient to count both together, and here both will be referred to as fin rays. Since the comparison of the two species by Günther (1860b) differences in numbers of dorsal and anal fin rays (*C. niger*, dorsal 39–41, anal 23–25; *C. britannicus*, dorsal 45, anal 30) have usually served to separate the species. The present range in data available to us is: *C. niger*, dorsal 35–41, anal 23–25; *C. britannicus*, dorsal 44–51 (with a 55 from an X-ray count by Nielsen (1963) and a doubtful 41 from Amanieu and Cazaux (1963), anal 25–33. Collett (1897) reported a specimen (b) of *C. niger* with 47 dorsal fin rays. In spite of the greater number of dorsal fin rays the dorsal base in this specimen was less (57.3% of standard length) than in specimen (a) with 41 dorsal fin rays (59.8%). Also the snout to dorsal in specimen (b) was longer (30.5%) compared with 28.4% for specimen (a), indicating that the dorsal was shorter in (b). Hence, it seemed likely that the dorsal fin ray count of 47 was an error, possibly a misprint. Collett's specimen (b) is now in the Trondheim Museum (Det Kongelige Norske Videnskabers Selskab Museet), has a length of ca. 44 cm, and is labelled Byneset, 1886. At our request it has been checked by Dr E. Sivertsen who reported by letter, May 15, 1965, that the number of dorsal fin rays, checked on the specimen and also by X-ray photograph, was not 47 but 37. Collett's specimen (a) is in the Zoological Museum of the University of Oslo and has been recently checked by Dr E. K. Barth and Collett's dorsal fin ray count of 41 confirmed (May 18, 1965). The first of Saemundsson's specimens of *C. britannicus* from Iceland had an anal ray count of 25 but all others were in the range 27–33.

Pectoral fin ray counts for *C. niger* have a range of 20–23 with 21–22 the most common. In *C. britannicus* there is a range of 18–21 (one, 16) with 20–21 the most common. The pelvic fin usually has six elements in both species (occasionally seven in *C. britannicus*). The caudal has 17 principal rays in both species (15 branched rays, 8 above and 7 below + 2 long unbranched). Caudal ray counts considerably different in number have probably resulted from counting additional or less rays. The numbers of scales in the lateral line overlap in the few individuals for which this difficult count was made. Vertebral numbers are 25 (10 + 14 + 1) in both species. The typical number of branchiostegal rays is 7. The number of gill-rakers on the lower limb of the first arch in the few specimens examined for this character is 13–15 in *C. niger*, and 11–13 in *C. britannicus*. Pyloric caeca numbers overlap. None of these characters provides a sure means of separating the species.

BODY PROPORTIONS

Allometric changes are very marked in at least *C. niger*, and therefore in considering body proportions due consideration should be given to the size of the fish. The use of any body proportion as the only criterion for identification is a very risky procedure.

In *C. niger* (Table IV and Fig. 6) where the range of fish sizes extends from 147 to 1065 mm S.L., marked negative allometry (in relation to S.L.) with increase in size is indicated for the head, snout, upper jaw, predorsal, pectoral, and ventral fin lengths, the eye diameter and the interorbital width. The allometric changes, however, are most evident in the lower part of the size range. In *C. britannicus* (Table V and Fig. 6) the small range of sizes, extending only from 258 to 435 S.L., and the production of the 10 sets of measurements by seven different scientists do not allow allometric differences to be revealed. In *C. niger*, if only these sizes were available in Table IV, allometric differences would also not be evident since the greatest changes noted are at smaller sizes. A difficulty with many measurements is that the method of making the measurements or the condition of the fish when measured is rarely stated. Furthermore, all measurements are perhaps not taken in a uniform way. In all our comparisons below, unless otherwise stated, body proportions are expressed as percentages of standard length.

Head length. The head length in *C. britannicus* is supposed to be relatively shorter than that in *C. niger* (head in *C. britannicus* $\frac{1}{6}$ and in *C. niger* $\frac{1}{5}$ total length, Günther, 1860b). Nielsen (1963) says that *C. britannicus* may be recognized in having a shorter head than *C. niger*.

The head length (Fig. 5, Tables IV and V, Item 4) in all specimens measured by us is 22.3–29.3 (average 24.7) for eight specimens of *C. niger*, and 20.6–22.8 (average 21.8) for five specimens of *C. britannicus*. The range for all specimens whose standard and head lengths are available to us is 20.0–29.3 (average 24.0) for 14 *C. niger* and 20.1–22.8 (average 21.5) for 10 *C. britannicus*. The *C. niger* ranges and averages are somewhat inflated by the inclusion of several fish smaller than the smallest *C. britannicus* but even allowing for this Günther's original observation that *C. britannicus* has a smaller head (on the average) is borne out. But there is enough overlap with *C. niger* to make the distinguishing of all individuals of the two species by head lengths impossible. More specimens, and especially smaller specimens of *C. britannicus*, are needed to outline the ranges more distinctly. It is even possible, judging from the decrease in standard length from 469 to 443 mm of the specimen of Bigelow and Schroeder (1937) measured by the second author many years later, that standard length may decrease with long preservation in alcohol. The body proportions will not necessarily change at the same rate. This could lead to a widening of the range in head length if some fish are measured fresh or only recently preserved and others after long periods of preservation.

Length of upper jaw relative to length of head. The length of the upper jaw relative to the length of the head (Tables IV and V, Item 8A) indicates a possible difference: 34.2–38.3 for 10 specimens of *C. niger* and 37.5–40.0

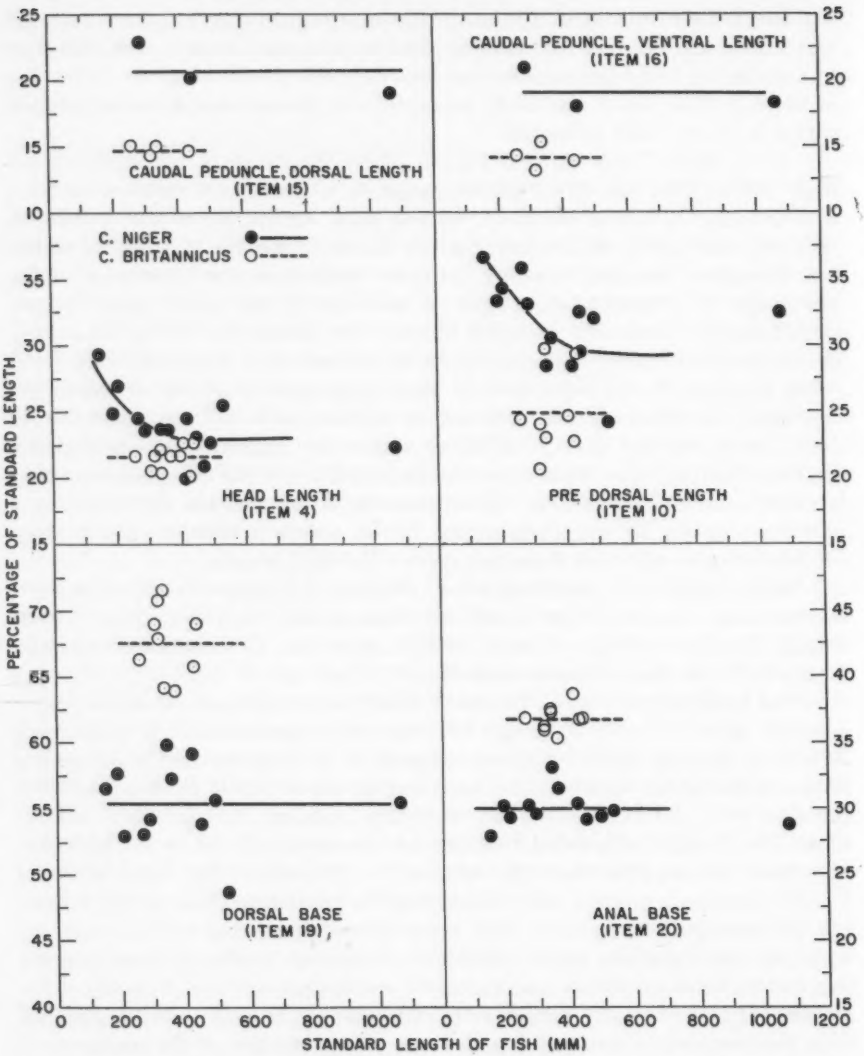

FIG. 6. Some body proportions of *Centrolophus niger* and *C. britannicus* relative to the standard length. (The items named are from Tables IV and V.)

for five specimens of *C. britannicus*, but Saemundsson's 1913 specimen of *C. britannicus* is far below this range with 31.3. Again, there is too much overlap for this characteristic to be useful for species separation.

Measurements involving the dorsal and anal fins (*Fig. 5, Tables IV and V*). Günther (1860b) gives the length of the dorsal and anal fins, respectively, as

$1\frac{4}{5}$ and $3\frac{1}{3}$ times in the total length (55.5 and 30.0% total length) for *C. britannicus* and $2\frac{1}{8}$ and $3\frac{3}{5}$ times in the total length (47.1 and 27.7% total length) for *C. niger*. Thus, both fin bases are relatively longer in *C. britannicus*. Regan (1902), however, examining the same specimen of *britannicus*, says that the anal base is relatively shorter in *C. britannicus* than in *C. niger*. This is unlikely because *C. britannicus* has a larger number of rays in the anal fin. Regan's observation may have been due to the poor condition of the stuffed type of *britannicus* which he was examining. The length of the base of the dorsal fin (Item 19), usually 52.9–59.8 (with Grieg's, 1911, specimen 48.7) for *C. niger* and 63.9–71.5 for *C. britannicus*, could be used to separate the two species. In these fin measurements different workers might choose different departure points for the beginning of the fin. In our specimens the bases of the dorsal and anal fins were measured from the anterior border of the structural base of the first ray (spine) to the point where the membrane behind the last ray contacts the body. Since the anteriormost fin elements become buried in the skin with growth in both *C. niger* and *C. britannicus*, the first point may be difficult to find. The greater length of the base of the dorsal in *britannicus* is in accordance also with the greater number of dorsal fin rays in this species.

A concomitant feature is the usually greater distance in *C. niger* from the snout to the anterior base of the dorsal fin (Item 10), 28.4–36.7 (with a low value of 24.2 by Grieg, 1911) in *C. niger* compared with 20.6–29.7 in *C. britannicus*.

The base of the anal fin (Item 20), which has more fin rays in *C. britannicus*, is also longer in this species (35.3–37.3) than in *C. niger* (27.9–33.1).

Greatest body height. Body height is one of the characters previously used for separating *C. britannicus* and *C. niger*: height of body $\frac{1}{5}$ of total length for *C. britannicus* and $\frac{1}{4}$ of the total length for *C. niger* (Günther, 1860b). Hence height of *britannicus* should be less than that of *niger*. Regan (1902), who had only Günther's specimen of *C. britannicus*, also says the body is more elongate in *britannicus*. This low height for *britannicus* is partly due to the poor condition of the stuffed specimen which had its length increased by 3 inches ($7\frac{1}{2}$ cm) by the stuffing (Day, 1880). Nielsen (1963), however, says that in fact *C. britannicus* can be recognized by the relatively *higher* body.

In our measurements we took body height as the greatest height, including the bases of the fins but not the fins themselves (Tables IV and V, Item 12). Our 5 *C. britannicus* were definitely higher (28.9–34.0, average 31.9) compared with our 8 *C. niger* (25.7–30.6, average 27.4). The range in the available 14 measurements is 25.7–30.6 (average 27.4) for *C. niger* and 28.4–38.1 (average 31.5) for the 10 *C. britannicus*, supposing that Nielsen's height at anus was also the greatest body height (see Fig. 1, 3 and Nielsen's plate V comparing the two species). On the average, body height in *C. britannicus* is greater than in *C. niger*, but the ranges overlap, would very likely overlap more with a greater number of specimens, and cannot be used at present for separating the species. The height of the body at the anus is also worth comparing but there are too few data at present.

Least height and length of caudal peduncle. Nielsen (1963) says that *C. britannicus* has a thicker and shorter caudal peduncle than *C. niger*. This is evident in his plate V. If, however, Saemundsson's (1913) figure of *C. britannicus* (also in Le Gall, 1933) is compared with that of Goode and Bean (1896) for *C. niger* (also in Le Gall, 1937) the least height of the caudal peduncle in Goode and Bean's figure of *C. niger* is relatively much greater than that in Saemundsson's figure of *C. britannicus*. In our specimens (Tables IV and V, Item 14) this least height measurement was 7.3–9.0 for *C. niger* and 7.6–9.2 for *C. britannicus*. Including all specimens noted the range for *C. niger* is 7.3–9.5 and that for *C. britannicus* 6.0–9.4. This character is much too variable to be used for separation of the species.

The length of the caudal peduncle from the posterior ends of the dorsal and anal fins to the mid-base of the caudal fin (Fig. 6, Tables IV and V, Items 15, 16) is distinctly greater in five specimens of *C. niger* (19.0–22.9 dorsal, 18.0–20.8 ventral) than in four specimens of *C. britannicus* (14.3–15.1 dorsal, 13.2–15.3 ventral). This is probably a useful difference for species separation. It is also apparent in the photographs in plate V of Nielsen (1963) and in the drawings in plate XL of Day (1880).

Greatest thickness. Nielsen (1963) says that, compared with *C. niger*, *C. britannicus* has a very thin body. The range in body thickness (Tables IV and V, Item 17) is 10.6–12.6 (average 11.7) for four specimens of *C. niger* and 5.7–11.2 (average 8.5) for seven specimens of *C. britannicus*. Thus, *C. britannicus* may be thinner on the average, but there is too much overlap for this character to be used to separate the species.

Relationship between beginning of dorsal fin and vertical from bases of pectoral and pelvic fins. Goode and Bean (1896), Duncker and Mohr (1929), and Le Gall (1937) all give as a characteristic of *C. niger* that the dorsal begins over the first third of the pectoral. The latter author uses this as a key character for distinguishing *C. niger* from *C. britannicus*.

For *C. britannicus* Günther (1860b) says that the beginning of the dorsal is in line with the vertical from the base of the pelvics. Duncker and Mohr (1929) use dorsal beginning over or in front of the pectoral base as a key character.

In our specimens the origin of the dorsal is behind the anterior (dorsal) base of the pectoral in *C. niger* and in front of or over the anterior (dorsal) base of the pectoral in *C. britannicus*. The dorsal fin in *C. britannicus* is usually longer and is closer to the snout than in *C. niger*, and usually begins further forward than that of *C. niger* in relation to the verticals from the bases of the pectorals and pelvics.

Lateral line. Regan (1902) uses the lateral line as one of the distinguishing features in his key for *Centrolophus* species: *C. britannicus* — lateral line with a short curve above the pectoral, thence running along the middle of the body; *C. niger* — lateral line with a rather long curve. This distinction in the lateral line is shown in the figure of *C. britannicus* by Saemundsson (1913), and that of *C. niger* by Goode and Bean (1896). We did not find this distinction

to be consistently useful for species separation. The lateral line in *C. britannicus*, however, appears as a more distinct and a whiter line (Fig. 1, 3, 4).

Firmness of body. This quality has not been mentioned in the literature. Our specimens of *C. niger*, usually preserved in formalin or alcohol, had firm solid bodies whereas specimens of *C. britannicus*, also preserved in formalin or alcohol, were soft and flabby, reminding the senior author of the jellied American plaice he had previously observed (Templeman and Andrews, 1956).

The skin of our *C. niger* was much tougher than that of *C. britannicus*. This was also observed by Fraser-Brunner (1935) who says that the integument of *C. britannicus* (one specimen observed fresh) is much softer and more fragile than that of *C. niger* (10 specimens observed fresh).

Colour. Günther (1860b) described *C. britannicus* as uniform brown and *C. niger* as uniform blackish or with irregular light spots. Colour descriptions by other authors show that a great deal of variation exists.

Some of these for *C. niger* are: dark brown (Regan, 1902); brown, clouded with lighter (Goode and Bean, 1896); covered with oblong spots, yellowish or very dark blue, nearly black, the ventral part silvery (Le Gall, 1937); black (Bigelow and Schroeder, 1937); bluish-black when fresh, faded to blackish-brown after storage in formalin for over a year (Scattergood and Coffin, 1953). Cuvier and Valenciennes (1833), from their own observations and those of Laurillard and Risso, describe *C. pompilus* (= *niger*) as varying in principal colours in different individuals and sizes from lead coloured and blackish to dark blue, often with greyish-yellow or dark spots on the sides and light leaden colour or silvery below. Fraser-Brunner (1935), who observed 10 specimens of *C. niger* and one of *C. britannicus* in the fresh condition, says for *C. niger* that the two males were smaller than the eight females and differed considerably in coloration. The background colour in both sexes was deep slate-blue but in the male each scale above the lateral line had a white centre, these spots forming horizontal white streaks, while on the side below the lateral line there were larger ovate white blotches. The head in the males had considerably more white than in the females. All the scales were tipped with black in the female, giving a speckled appearance; there were no white marks and the caudal fin was usually much darker. Our Grand Bank specimen of *C. niger* after preservation in formalin for 5 years was darkish grey, a little lighter below, fins black, inside mouth and gill cover dark, posterior edges of scale pockets black, peritoneum yellowish-white with light grey areas.

For *C. britannicus* some of the descriptions of colour are: uniform dark-chocolate-brown (Saemundsson, 1913); uniform brown (Le Gall, 1933); the colour in life is brown, with each scale edged with black and the head entirely white (Fraser-Brunner, 1935). In three of our individuals of this species after preservation for 5–6 years in formalin the colours were: light brown, tips of fins dark, inside mouth and gill cover grey to dark, internal body lining black (Table II, No. 32); grey, tips of fins darker, darker spots around edges of scale pockets, inside of mouth and gill covers and body cavity black (Table II, No. 35 and 36).

Thus, although we have the possibility of colour distinctions, the use of colour differences as a method of separating the two species is in a rather confused state at present. The peritoneum of *C. britannicus* is, however, usually dark and that of *C. niger* usually light — a good distinction. Also, in the great majority of the *C. britannicus* we have seen, the thin epidermis has been scraped from the head, giving it a whitish or pinkish appearance. This condition has rarely been observed by us in *C. niger*.

FOOD

From our specimens of *C. britannicus* three stomachs were available for examination. One stomach was empty. Another (Table II, No 37) contained 4 cc of euphausiid fragments and three hyperiid amphipods, *Euthemisto* sp., indicating pelagic feeding. A third (Table II, No. 45) contained five hyperiid amphipods, *Euthemisto* sp., which were probably eaten in the net.

The large specimen of *C. niger* (Table I, No. 8), caught on longline with squid bait, had the squid in its stomach. Collett (1896) says that the stomach of a 212-mm *C. pompilus* (*C. niger*), taken at the surface west of Florès, Azores, was filled with a siphonophore, and some individuals of a hyperiid amphipod.

ACKNOWLEDGMENTS

The authors are grateful to Dr Hubert J. Squires who received and recorded the Newfoundland specimens at the St. John's Station, to Mr V. M. Hodder and the captains of three Newfoundland trawlers for the four specimens of *C. britannicus* and one specimen of *C. niger* brought to the St. John's Station, to Mr William C. Schroeder, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts and the crew of the trawler *Storm*, Rockland, Maine, for a specimen of *C. britannicus*, and to Mr Martin R. Bartlett, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, for the large specimen of *C. niger* and its photograph. The following individuals, to whom we extend our thanks, made museum specimens available and aided in a number of ways: Dr P. H. Greenwood and Mrs Alwynne C. Wheeler, British Museum (Natural History), London, Dr Giles W. Mead, Museum of Comparative Zoology, Harvard, Mme M. Bauchot and Dr M. Blanc, Muséum Nationale d'Histoire Naturelle, Paris, and Dr Leonard P. Schultz and Mr Nathaniel Gramblin, United States National Museum, Washington, D.C. Thanks are also due to Mr Jørgen Nielsen, Universitetets Zoologiske Museum, Copenhagen, for information on *C. britannicus* including two new records, to Sir Frederick S. Russell, Marine Biological Association of the United Kingdom, The Laboratory, Plymouth, for information on *C. britannicus* and for supplying two new records of *C. niger*, to Dr Paul M. Hansen, Ministeriet for Grønland, Grønlands Fiskeriundersøgelser, Charlottenlund, for information on the Greenland area, to Mr Jón Jónsson, The University Research Institute, Department of Fisheries, Reykjavik, for information on the Icelandic area, to Dr G. Krefft,

Bundesforschungsanstalt für Fischerei, Institut für Seefischerei, Hamburg, for a new record of *C. britannicus*, and to Dr Erling Sivertsen, Det Kongelige Norske Videnskabers Selskab Museet, Trondheim, Dr Edward K. Barth, Zoological Museum, University of Oslo, Oslo, and Mr Steinar Olsen, Fiskeridirektoratets Havforskningsinstitutt, Bergen, for information on *C. niger* from the Norwegian area. We are grateful to Dr E. Bertelsen, Danmarks Fiskeri-og Havundersøgelser, Charlottenlund, for making available the two *Dana* specimens of *C. niger*.

The second author's work was supported by a grant from the Committee on Evolutionary Biology, Harvard University, by National Science Foundation Grant G-F 147 to Harvard University, and by a Woods Hole Oceanographic Institution Predoctoral Fellowship.

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Oxygen Dissociation Curves of the Blood of Atlantic Salmon (*Salmo salar*) Acclimated to Summer and Winter Temperatures[1]

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ABSTRACT

Oxygen dissociation curves were constructed at three tensions of carbon dioxide, viz: 0–1 mm Hg, 10 mm Hg, and 40 mm Hg; and at five temperatures: 0, 5, 15, 20, and 25 C. Carbon dioxide dissociation curves were constructed at 5 C only. Gas tensions in mixed venous blood were determined for four salmon at 5 C. Oxygen dissociation curves at three temperatures were carried out for fish acclimated to summer and winter conditions.

The physiological function of the blood of Atlantic salmon (*Salmo salar*) is well adapted for the range of temperatures encountered. As is the case for other salmonids, the adverse effect of low temperature is opposed by an increased sensitivity of the blood to carbon dioxide. No influence of acclimation was observed for the effect of carbon dioxide on the equilibrium between oxygen and hemoglobin.

INTRODUCTION

Barcroft and King (1909) were the first to demonstrate the influence of temperature upon the equilibrium between oxygen and homoglobin. Krogh and Leitch (1919) showed that the increased affinity of the blood of certain fish for oxygen with decreasing temperatures is associated with an increased sensitivity of the oxygen–hemoglobin equilibrium to carbon dioxide. Black et al. (1966) showed that there was a pronounced Bohr effect in the blood of the brook trout (*Salvelinus fontinalis*) as well as an increasing affinity of the blood for oxygen with decreasing temperature. It was also found that the properties of hemoglobin, with regard to the effects of temperature and carbon dioxide on the affinity of the blood for oxygen, were identical throughout the year. The pioneer investigation of the seasonal effect on fish blood was carried out by Kawamoto (1929). He studied the effect of temperature and relative red cell volume upon the hemoglobin dissociation curve.

The present paper deals with the oxygen dissociation curves of the Atlantic salmon carried out both during the summer and winter at various temperatures and tensions of carbon dioxide.

METHODS

Stocks of salmon were held in two places: the Bedford Hatchery in Bedford, N. S., and in the salmon rearing station at Grand Lake, N. S. Both stations

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J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

are operated by the Department of Fisheries of Canada. The salmon at Grand Lake were originally transported from the Bedford hatchery at the beginning of the investigation. Water temperatures at the Bedford hatchery, during the fall and spring, ranged from 0 to 22 C, while the temperatures at Grand Lake during the spring and summer were between 5 and 20 C. No fish died during the experiments on winter-acclimated fish at Bedford, but up to half the salmon at Grand Lake were lost during the summer.

Methods and procedures for taking blood samples, making up gas mixtures, equilibration, and analyses were those described in earlier papers by Black (1940) and Black et al. (1966).

Samples of blood from summer-acclimated fish were taken at Grand Lake and transported to Dalhousie University for analyses. The journey occupied $1\frac{1}{4}$ hr. For winter-acclimated fish blood samples were taken at Bedford; 1 hr elapsed between cardiac puncture and analyses. During this time the blood was stored in the syringe and embedded in ice, 1 ml of liquid heparin (Connaught Laboratories) was used for each 20 ml of blood. Samples were pooled in only one instance of 35 experiments.

RESULTS AND DISCUSSION

Oxygen Capacities and Red Cell Volumes

The average oxygen capacities, red cell volumes (hematocrits), and the average oxygen capacities of 100 ml red blood cells for Atlantic salmon acclimated to summer and winter conditions together with the data for the combined seasons are presented in Table I. The data of Benditt et al. (1941) are also included for freshwater Atlantic salmon captured by hook and line.

Table I. Combined summary of the oxygen capacities and red cell volumes for Atlantic salmon (*Salmo salar*) corrected for heparin dilution, and the oxygen capacities of 100 ml of red blood cells.

Season		Number of determinations	Oxygen capacity (*vol %*)	Number of determinations	Red cell volume (%)	Oxygen capacity of 100 ml cells (*vol %*)
Summer	Average ± SE	13	8.3±0.67	12	23.2±1.70	36.5±1.76
	Range		4.5–12.1		16.4–33.2	26.3–49.2
Winter	Average ± SE	22	11.2±0.51	22	27.9±1.33	40.7±1.45
	Range		5.8–15.8		13.3–39.9	29.4–65.0
Combined seasons	Average ± SE	35	10.1±0.46	34	26.3±1.11	39.2±1.16
	Range		4.5–15.8		13.3–39.9	26.3–65.0
Summer (data of Benditt et al., 1941)	Average ± SE	6	8.8	6	24.8	35.5
	Range		6.7–10.1		19.3–28.4	

The average oxygen capacity for the summer condition (8.3 volumes per cent) is significantly lower than the value of 11.2 volumes per cent obtained in winter ($P < 0.05$). The average red cell volume, while lower in summer, is not significantly lower. The average oxygen capacity reported by Benditt et al. (1941) for freshwater fish acclimated to summer conditions is 8.8 volumes per cent compared with 8.3 volumes per cent reported here. Oxygen capacity values for 100 ml red blood cells obtained in summer and winter are alike. These averages are concordant with those of other fish reviewed by Redfield (1933).

Oxygen Dissociation Curves

Effect of Temperature and Carbon Dioxide

Oxygen dissociation curves were constructed for blood at 0 C (Fig. 1), 5 C (Fig. 2), 15 C (Fig. 3), 20 C (Fig. 4), and 25 C (Fig. 5). Blood was obtained by cardiac puncture from fish acclimated to either winter or summer conditions except in the case of dissociation curves constructed at 5 C. In this instance all blood samples came from fish acclimated to winter conditions.

The water temperature in which the fish acclimated to winter conditions lived was approximately 5 C, whereas that for summer-acclimated fish was approximately 20 C.

Blood carbon dioxide dissociation curves for oxygenated and deoxygenated blood were also constructed at 5 C for fish acclimated to winter conditions (Table II, Fig. 6 and 7).

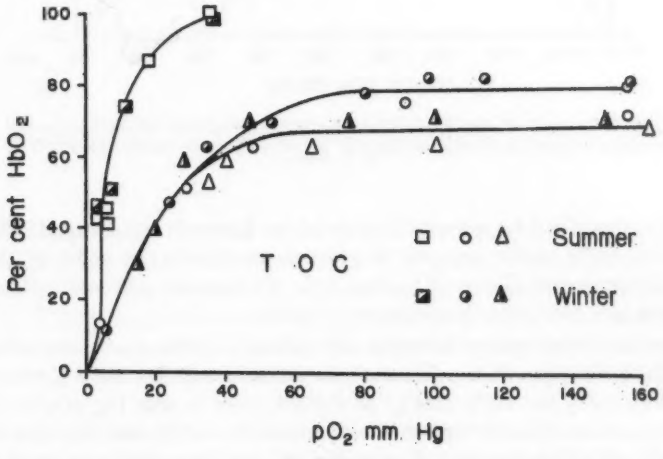

Fig. 1. Oxygen dissociation curves for Atlantic salmon blood acclimated to summer and winter conditions at various tensions of carbon dioxide, equilibrated at 0 C.

TABLE II. Venous blood gases for Alantic salmon (*Salmo salar*) acclimated to winter conditions at 5 C.

Experiment	Carbon dioxide (*vol %*)	Oxygen (*vol %*)	Oxygen capacity (*vol %*)	HbO_2 (%)	pCO_2 (*mm Hg*)	pO_2 (*mm Hg*)
Dec. 14, 1945						
A	20.1	5.1	9.6	53	5.8	16
B	13.7	4.8	8.8	55	2.6	14
Dec. 31, 1945						
A	23.4	2.5	8.9	28	7.5	11
B	16.9	2.5	5.5	46	5.0	15

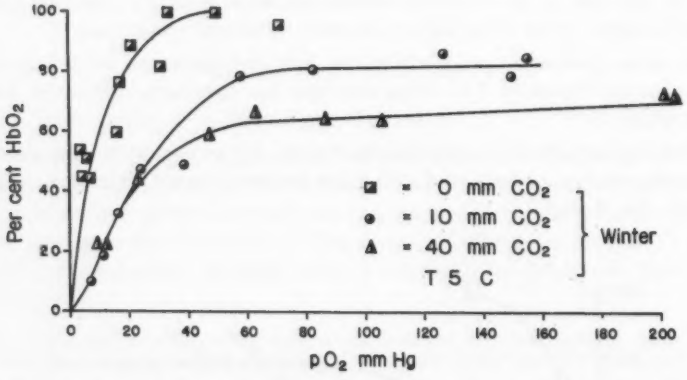

FIG. 2. Oxygen dissociation curves for Atlantic salmon blood acclimated to winter conditions at various tensions of carbon dioxide, equilibrated at 5 C.

As first described for mammalian blood by Barcroft and King (1909), there is a marked shift of the oxygen dissociation curves to the right as the temperature is increased (Table III, Fig. 1–5). The values are lower than those of Irving et al. (1941) for three species of trout.

There is a very great influence of carbon dioxide upon the affinity of hemoglobin for oxygen in the blood of the Atlantic salmon. At 0 C the tension of unloading (pO_2 for 50% HbO_2) is shifted from 5 mm Hg pO_2 to 26 mm Hg pO_2 by an increase in carbon dioxide from 1 to 10 mm Hg (Table III). At 15 C the shift is from 10 to 36 mm Hg pO_2 for the same increase of carbon dioxide. The hemoglobin fails to attain 100% saturation in the presence of 40 mm Hg pCO_2 even when the pO_2 is 150 mm Hg.

TABLE III. Tensions of unloading ($t\mu$ = pO_2 for HbO_2 of 50%) for oxygen in Atlantic salmon (*Salmo salar*) blood equilibrated at five different temperatures and three different tensions of carbon dioxide.

Temperature	pCO_2	pCO_2	pCO_2
(*C*)	(*0–1 mm Hg*)	(*10 mm Hg*)	(*40 mm Hg*)
0	5	26	26
5	7.5	27	31
15	10	36	46
20	15	46	55
25	17	29	45

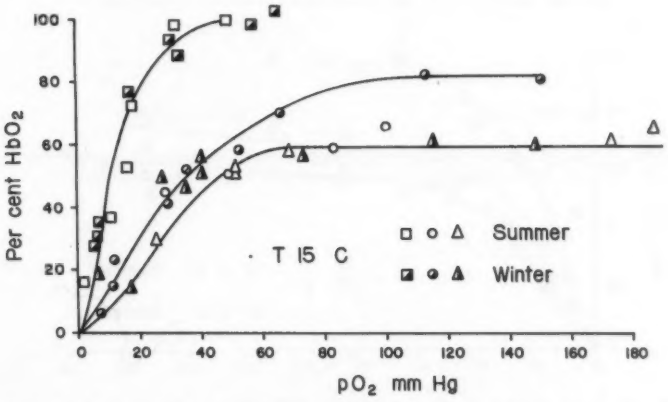

FIG. 3. Oxygen dissociation curves for Atlantic salmon blood acclimated to summer and winter conditions at various tensions of carbon dioxide, equilibrated at 15 C.

There appears to be some variability in the data for 0–1 mm Hg pCO_2 at 5 C (Fig. 2) but in all other curves (Fig. 1, 3, 4, and 5) there is little variation in the data. At pCO_2 10 mm Hg, the curves show marked variability at 15 and 25 C (Fig. 3, 5). Similar variability of oxygen affinity was observed in the oxygen dissociation curves of brook trout at the same tension of carbon dioxide (Black et al., 1966). No satisfactory explanation can be offered for this variability.

An examination of the data reveals no consistent difference in the Bohr effect taken from fish acclimated to summer or winter conditions. Black et al. (1966) found no correlation between the Bohr effect and acclimation to temperature in the blood of brook trout.

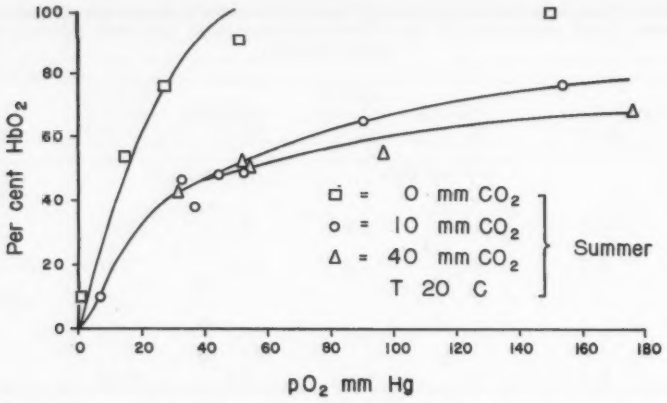

FIG. 4. Oxygen dissociation curves for Atlantic salmon blood acclimated to summer conditions at various tensions of carbon dioxide at 20 C.

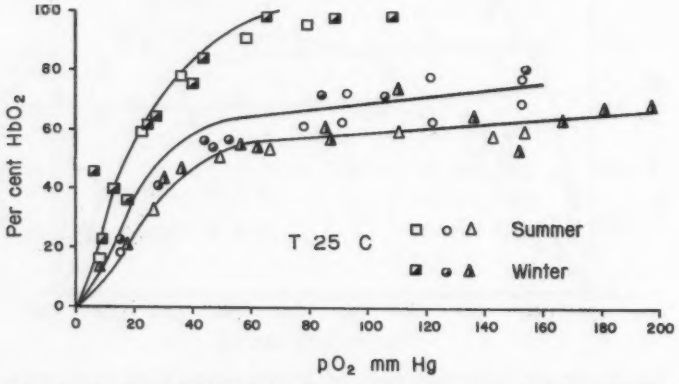

FIG. 5. Oxygen dissociation curves for Atlantic salmon blood acclimated to summer and winter conditions at various tensions of carbon dioxide at 25 C.

Krogh and Leitch (1919) realized that the high affinity of the blood for oxygen at low temperatures would prevent the release of oxygen from the blood to the tissues, except if the tissues were hypoxic. The large Bohr effect of fish blood, however, balances the high oxygen affinity and enhances oxygen delivery to the tissues. Root (1931) later demonstrated that several species of marine fish possessed a large Bohr effect, and Black (1940) found a gradation in the Bohr effect in freshwater fish, which appeared to be related to differences in environmental temperatures.

The Bohr effect in the Atlantic salmon is of such a magnitude at 0 C, that at 10 mm Hg pCO_2, three-quarters of the load of oxygen would be discharged to the tissues with the pressure of oxygen maintained above 12 mm

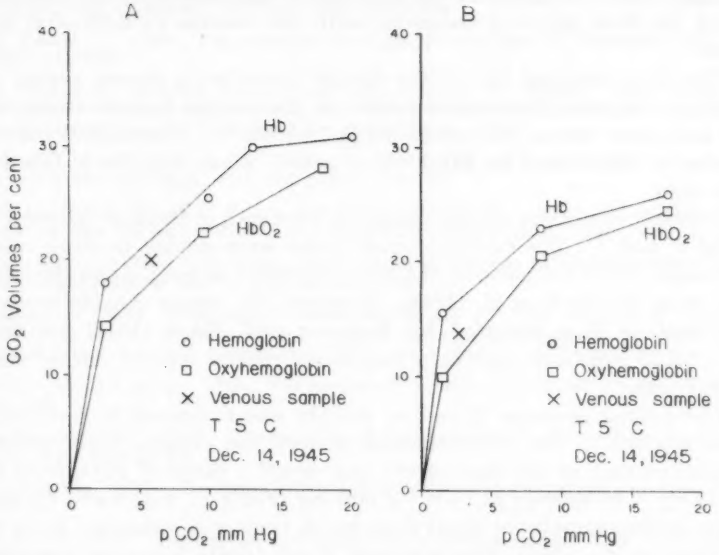

FIG. 6. Carbon dioxide dissociation curves for Atlantic salmon blood acclimated to winter conditions and equilibrated at 5 C (December 14, 1945).

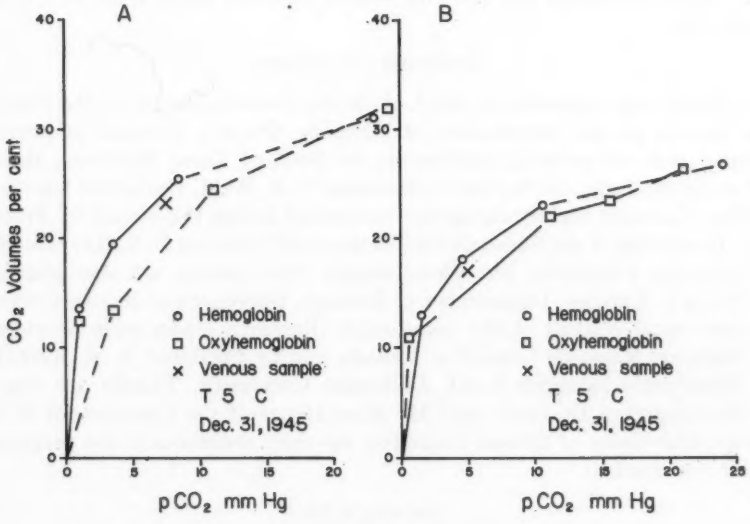

FIG. 7. Carbon dioxide dissociation curves for Atlantic salmon blood acclimated to winter conditions and equilibrated at 5 C (December 31, 1945).

Hg. Riggs (1951) investigated the Bohr effect and discovered that the magnitude of the Bohr effect is associated with the number of sulfhydryl groups present.

The data obtained for carbon dioxide dissociation curves appear to be consistent over the physiological section of the curves, but are erratic at the lower and upper ends of the curves in Fig. 7 (A and B). The range of the curves is similar to that found by Black et al. (1966) in two samples of blood from brook trout.

A sample of venous blood was analysed for each of the four salmon (Table II, Fig. 6 and 7). The carbon dioxide levels were similar to those reported by Itazawa (1957) for blood of the carp (*Cyprinus carpio* L.) and the blood of brook trout by Black et al. (1966). However, the carbon dioxide levels were about half of those reported by Ferguson and Black (1941) for rainbow trout (*Salmo gairdneri*) and carp acclimated to and studied during summer temperatures.

The partial pressure of carbon dioxide was estimated by referring the venous content to the carbon dioxide dissociation curves. These points are indicated on each of the four curves and reveal a range of pCO_2 from 2.5 to 7.5 mm Hg. The average pCO_2 is 5.2 mm Hg (Table II, Fig. 6 and 7). Venous tension for two samples of blood from brook trout was estimated to be 6 mm Hg (Black et al., 1966). Ferguson and Black (1941) found an average of 9 mm Hg pCO_2 in four samples of blood from rainbow trout acclimated to summer conditions.

The partial pressure of oxygen averaged 14 mm Hg (Table II). Black et al. (1966) estimated the ppO_2 in venous blood of brook trout at 0 C to be 15 mm Hg.

ACKNOWLEDGMENTS

Thanks are expressed to Mr J. A. Rodd, former director of the Fish Culture Branch of the Department of Fisheries, Ottawa, Canada, in providing live material and working facilities at the Bedford Trout Hatchery, Bedford, and at Grand Lake, N. S.; and to Professor C.B. Weld, Dalhousie University, Halifax. Criticism and encouragement extended during the project by Professor A. G. Huntsman of the University of Toronto and Professor F. R. Hayes formerly of Dalhousie University are acknowledged. The authors are also grateful to Dr David J. Randall, Department of Zoology, University of British Columbia, for his critical reading of the manuscript. Research grants were provided by the National Research Council of Canada and by President A. E. Kerr, from the President's Research Fund, Dalhousie University. Thanks are also due to Miss Georgina Docherty and Mr Kurt Henze of the Department of Physiology, University of British Columbia, for their assistance in the preparation of this manuscript.

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Sea-Floor Conditions Around the Magdalen Islands in the Southern Gulf of St. Lawrence[1,2]

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ABSTRACT

Acoustical, underwater photographic, and bottom sediment sampling data indicated that the major geomorphological features of the shelf throughout the southern Gulf of St. Lawrence are not related to the present environmental conditions. Submarine troughs and tunnel valleys give ample morphological evidence of extensive Pleistocene glaciation. Bottom samples and acoustical records revealed that sandstone bedrock with an intermittent veneer of sediments occurs on the sea floor between Prince Edward Island and the Magdalen Islands, as well as to the north of the Magdalen Islands. In contrast, the shelf areas west and east of the Magdalen Islands have an almost continuous sediment cover with only small exposures of bedrock. These sediments are considered to be mainly the erosional products of the local bedrock. Areas of elevated bottom relief such as Bradelle Bank are bedrock elevations on top of which there is a nearly continuous but relatively thin sediment cover. A submarine terrace between approximately 28 and 34 fath, well developed around the Magdalen Islands, is considered to mark a former sea level.

INTRODUCTION

A study of the recent depositional conditions in the St. Lawrence submarine valley (Nota and Loring, 1964) revealed marked differences in geomorphology between that area and the southern Gulf. This difference was sharp enough to suggest that the two areas ought to be treated separately. The present contribution is therefore directed to consideration of the general morphological features of the southern Gulf area with special emphasis on morphology and sediments of the shelf around the Magdalen Islands. It is one of a series of investigations of the whole area which were initiated by the Atlantic Oceanographic Group of the Fisheries Research Board of Canada in 1961.

There are no previous publications dealing with this area in detail, although reports by Loring et al. (unpublished data) and Loring and Lahey (unpublished data) have contributed background information. The following interpretations are based on bottom samples, echograms, Sparker records, asdic records, and underwater photographs. Field observations were made on board CNAV

[1]Received for publication February 11, 1966.

[2]This is the first of a series of papers on the southern Gulf of St. Lawrence. A paper dealing with the interrelationships between the submarine topography, sediment composition, sediment sources, present processes of deposition, and depositional history of this area is in preparation.

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J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

Sackville (1963: S-75; 1964: S-79; 1965: BIO-27-65). Additional information on surface bottom features was obtained from the use of subhorizontal asdic equipment on board CSS *Kapuskasing* during a cruise in July 1965.

GEOLOGICAL FRAMEWORK

The shelf of the southern Gulf forms a semicircular, shallow-water area lying southwest of the deep submarine valley known as the Laurentian Channel. The surrounding land area forms part of the Appalachian region of Canada (Weeks, 1963). This region as a whole is a gently southeasterly sloping upland dissected by valleys and broken by broader lowland areas developed on belts of weak rocks. The southern Gulf is bordered by the uplands and mountains of the Gaspé Peninsula to the northwest, the lowlands of New Brunswick, Prince Edward Island, and Nova Scotia to the south, and the highlands of Cape Breton Island to the east. The Magdalen Islands lie in the northeast corner of the area (Fig. 1).

The uplands and mountains of the Gaspé Peninsula reach elevations in excess of 4000 ft and are mainly underlain by Ordovician and Silurian limestones, slates, and quartzite. The lowlands of New Brunswick, Nova Scotia, and Prince Edward Island together with the Magdalen Islands form a single physiographic unit on which the elevations seldom exceed 400 ft. The lowlands are underlain by generally low dipping soft carboniferous sandstones, shales, and some coal measures, through which, particularly on the Magdalen Islands, small instrusive bodies of volcanic rocks cause prominent eminences (Weeks, 1963; Sanschagrin, 1964). The Cape Breton highlands present an almost plateau-like surface dissected in places by streams, and with elevations ranging between 1300 and 1500 ft. The highland region is mainly underlain by granitic and metamorphosed rocks of precarboniferous age. A narrow coastal strip of soft carboniferous rocks separates the harder, resistant rocks of the highlands from the sea in the southern corner of the study area.

SUBMARINE GEOMORPHOLOGY

Various charts and original work sheets of the Canadian Hydrographic Service, Marine Sciences Branch, Department of Mines and Technical Surveys, are the main sources of information on the submarine geomorphology of the area. These data were extended and corrected (Fig. 1,2) by means of new soundings obtained from echograms taken with a Kelvin Hughes Model 26B echosounder and a precision depth recorder installed on CNAV *Sackville*.

For purposes of discussion, a general outline of the submarine morphology of the southern Gulf as a whole is given first; following this, a more detailed description of the shelf around the Magdalen Islands is presented.

General Morphology of the Southern Gulf

The shelf of the southern Gulf exhibits an irregular relief and is characterized by the presence of elevated areas and trough-shaped depressions as

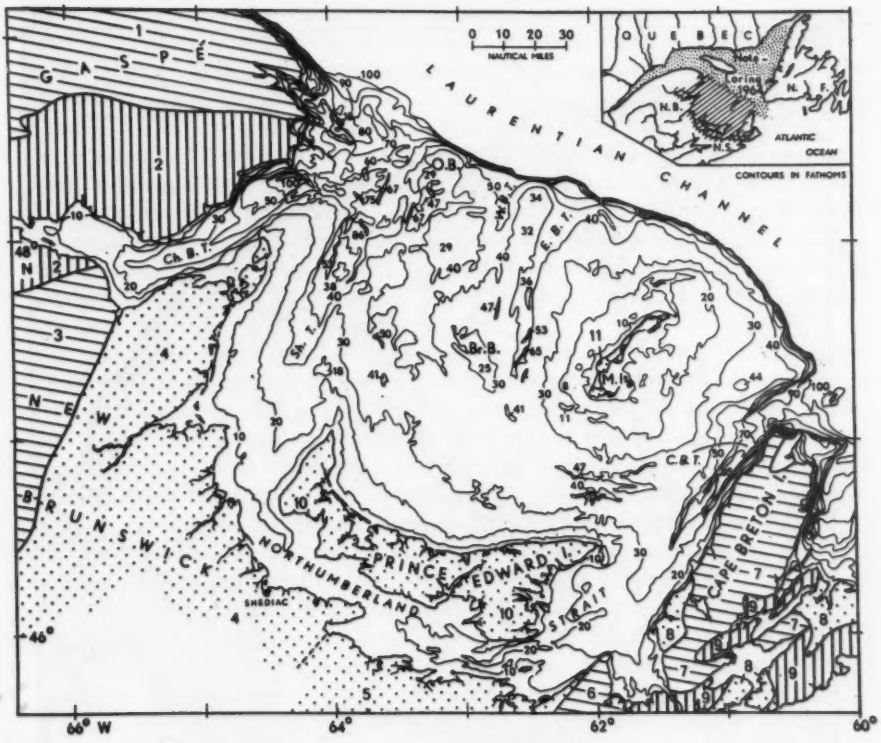

FIG. 1. Generalized geomorphological map of the entire southern Gulf region (after Weeks, 1963), with simplified bathymetry of the Magdalen Shallows. Ch. B.T. = Chaleur Bay trough; Sh.T. = Shediac trough; W.B.T. = Western Bradelle trough; E.B.T. = Eastern Bradelle trough; C.B.T. = Cape Breton trough; M.Is. = Magdalen Islands; Br.B. = Bradelle Bank; O.B. = Orphan Bank; 1 = Notre Dame Mountains; 2 = Chaleur Uplands; 3 = New Brunswick Highlands; 4 = New Brunswick Lowlands; 5 = Cumberland Lowlands; 6 = Antigonish Highlands; 7 = Cape Breton Highlands; 8 = Cape Breton Lowlands; 9 = Atlantic Uplands of Nova Scotia; 10 = Prince Edward Island Lowlands; 11 = Gulf of St. Lawrence Plain. Dotted area of insert map was discussed by Nota and Loring (1964).

the major morphological features. The incised shelf, usually referred to as the Magdalen Shallows (Lauzier, 1957) has an average depth of less than 40 fath. The width of the shelf, measured from the north coast of Prince Edward Island to the edge of the Laurentian Channel, varies between 90 and 120 nautical miles. Over this distance the average slope varies between 2.5 and 3.3 ft/mile.

The main features of positive bottom relief are the circular submarine platform on which the Magdalen Islands are situated and the elevated areas known as Bradelle Bank (west of the Magdalen Islands), Orphan Bank (in the northwest corner of the area), and some unnamed banks (see Fig. 1).

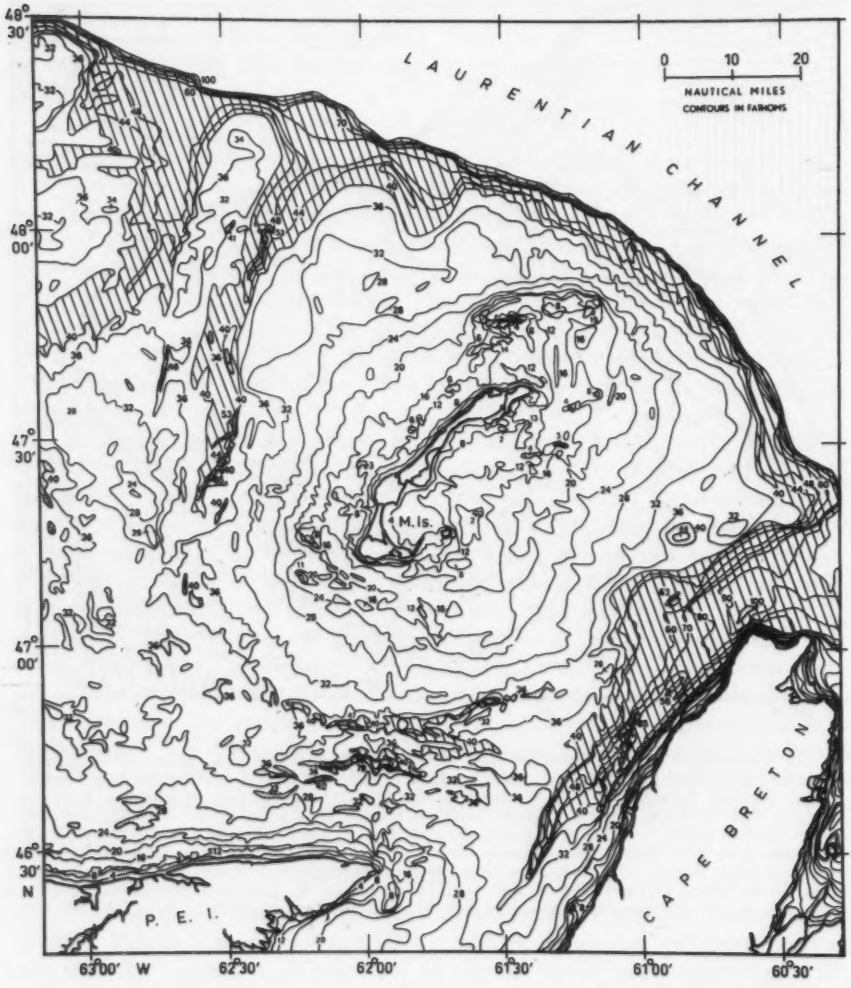

FIG. 2. Detailed bathymetry of the shelf area around the Magdalen Islands. Shaded areas indicate water depths greater than 40 fath. East Point, P.E.I. is located at 46°.26′N lat., 61°.58′W long.

To the west, the submarine extension of North Point, P.E.I. (47°03′N, 64°00′W) forms the most conspicuous morphological feature of positive relief.

In the northwestern corner of the southern Gulf, a distinctly trough-shaped submarine valley extends outwards from the Bay of Chaleur to join the Laurentian Channel off the Gaspé Peninsula (see Fig. 1). Off Gaspé, the

Chaleur Bay trough is joined from the south by another trough-shaped submarine valley referred to as the Shediac trough, which, acccording to the bathymetry, begins somewhere off Shediac, N.B., in the western part of the Northumberland Strait. In the east, off the coast of Cape Breton Island, there is another submarine valley with pronounced trough shape, which will be referred to as the Cape Breton trough. In the central part of the area two more submerged valleys extend northeasterly to join the Laurentian Channel. These trough-like valleys will be referred to here as the Western and Eastern Bradelle troughs, being separated from one another by Bradelle Bank. The trough-shape of the Western and Eastern Bradelle submarine valleys is less distinctive in outline than that of Chaleur Bay, Shediac, and Cape Breton troughs.

The submarine valleys neither in cross profile nor in long profile greatly resemble stream-carved valleys. Instead, they all have a broad base, large irregularly shaped rimmed depressions, oval-shaped elevations in their floors, and an undulating longitudinal profile. In addition, the Chaleur Bay and Cape Breton troughs show relatively steep walls. In contrast to river valleys, which usually have their tributary valleys joining them accordantly, the trough-shaped depressions mentioned form hanging valleys above the main trough, i.e. the Laurentian Channel. These characteristics are common in glaciated valleys, though individually they are not diagnostic of glaciation.

Nota and Loring (1964) discussed the submarine morphology and sediments of the Laurentian Channel and concluded that extensive Pleistocene glaciation largely determined its present shape. Heezen and Drake (1964) mention the presence of a red sediment in the Laurentian Channel buried under a grayish layer of varying thickness; they believe that the red deposit is of glacial origin. Nota and Loring (1964) found brownish gray surface sediments in the Laurentian Channel (e.g. stations S-56 – 6,7) and consider them as having most probably originated from the reworking of glacial drift. The present study of the southern Gulf reveals that low dipping bedrock of reddish-brown friable sandstone is exposed over large areas of the shelf (see Sediments). It is assumed that glacial erosion of the shelf, cutting trough-shaped depressions in the weak sandstone bedrock, had led to the accumulation of the reddish glacial deposits (till) in the Laurentian Channel, now buried under Recent, usually gray-colored sediments (see Nota and Loring, 1964, p. 206). The combination of all these features leaves little doubt that the present shape of the submarine troughs in the southern Gulf is related to Pleistocene glaciation. The postglacial transgression and recent depositional processes must have modified the Pleistocene morphology.

Morphology of Shelf Around the Magdalen Islands

The echograms of the shelf area around the Magdalen Islands show striking regional variations in sea floor characteristics (Fig. 3). The vertical scale was fixed at 120 ft equals 127 mm, assuming a sound velocity of 4800 ft/sec in sea water. The horizontal scale was variable either by changing the speed

of the paper through the recorder or by changing the ship's speed, or both. Continuous echograms were taken at a ship speed of about 8 knots and a high paper speed. Due to strongly varying weather conditions, both ship's speed and paper speed occasionally had to be adjusted to obtain the best possible records. Hence, in considering the records shown in Fig. 3, attention should be given to the fact that there is not a uniform vertical exaggeration. Additional information for the interpretation of the echograms was obtained from asdic records, bottom sampling, and bottom photographs. In reading the text, reference should be made to the bathymetric chart (Fig. 2) as well as to the individual profiles shown in Fig. 3.

Echograms obtained between Prince Edward Island and the Magdalen Islands show that the bottom topography in this area is rugged (Fig. 3, lines 2 and 3). This in turn indicates that bedrock is at or very near the surface and hence controls the surface expression of the sea floor. Bottom sampling, asdic surveys, and underwater photographs confirm this conclusion.

A major morphological feature is found about 15 miles north of East Point, P.E.I. (Fig. 2). The feature consists of two valley-shaped depressions that are elongated and subparallel in a west–east direction; the northernmost can be followed over a distance of about 30 nautical miles, and the southern about 15 nautical miles. The north–south width of each depression is about 2½ nautical miles. They are separated from each other by a topographic elevation in the west, while in the east they are partially interconnected. The valleys do not show a smoothly graded longitudinal profile; instead they are irregular and have a series of isolated basins which attain considerable depths. The deepest basin occurs in the southern depression and was found to be deeper than 75 fath. The position of the basins gives the valleys a somewhat winding, long profile. Echograms and bottom samples show that the slopes of the valleys have little or no sediment cover and are composed, for the most part, of reddish brown friable sandstone, similar in lithology to the bedrock exposed along the adjacent coast of Prince Edward Island. Sparker records obtained by a modified EGG Boomer system[4] indicate that the location of the southern valley is associated with a fault system. This particular morphology strongly suggests that the elongated valleys have resulted from the erosion of meltwater streams, in drainage tunnels at the base of the glacier ice. The ice must have been thick enough to provide the hydrostatic pressure for the water velocity necessary to erode sizable gorges in the substratum. Similar elongated valleys, though on a much smaller scale, occur west of the Magdalen Islands. Features of this kind have been described as tunnel valleys in North America (Wright and Ruhe, 1965) and as Rinnenseen in north Germany (Woldstedt, 1954, p. 374). A report on the submarine occurrence of similar features in the basin of the North Sea is given by Valentin (1957).

In contrast to the above part of the shelf, echograms from sections west of the Magdalen Islands (Fig. 3, lines 5, 8, and 13) show smooth bottom relief

[4]On loan through the courtesy of the Institute of Oceanography, Dalhousie University.

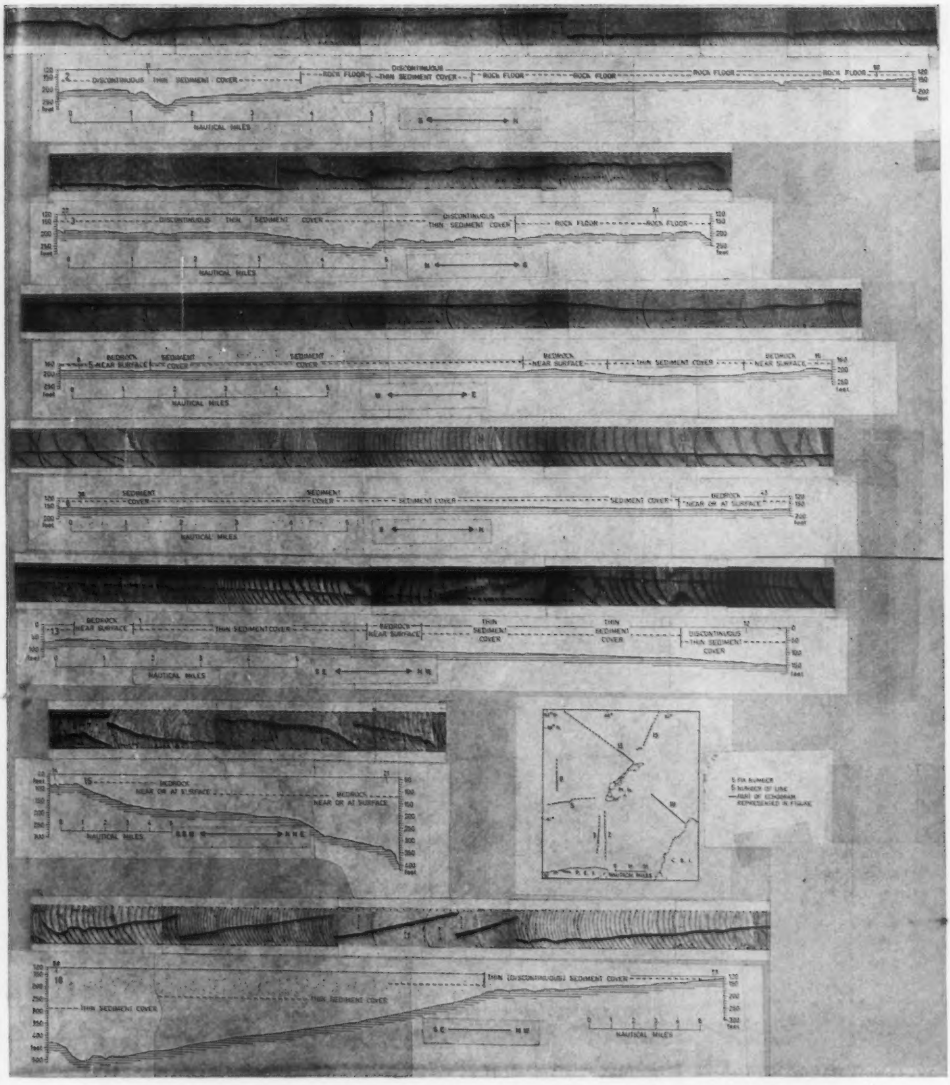

FIG. 3. Examples of acoustic reflexion profiles of shelf around the Magdalen Shallows. Each echogram is accompanied by a drawn profile with interpretation. Note that the vertical exaggeration is not uniform (see text).

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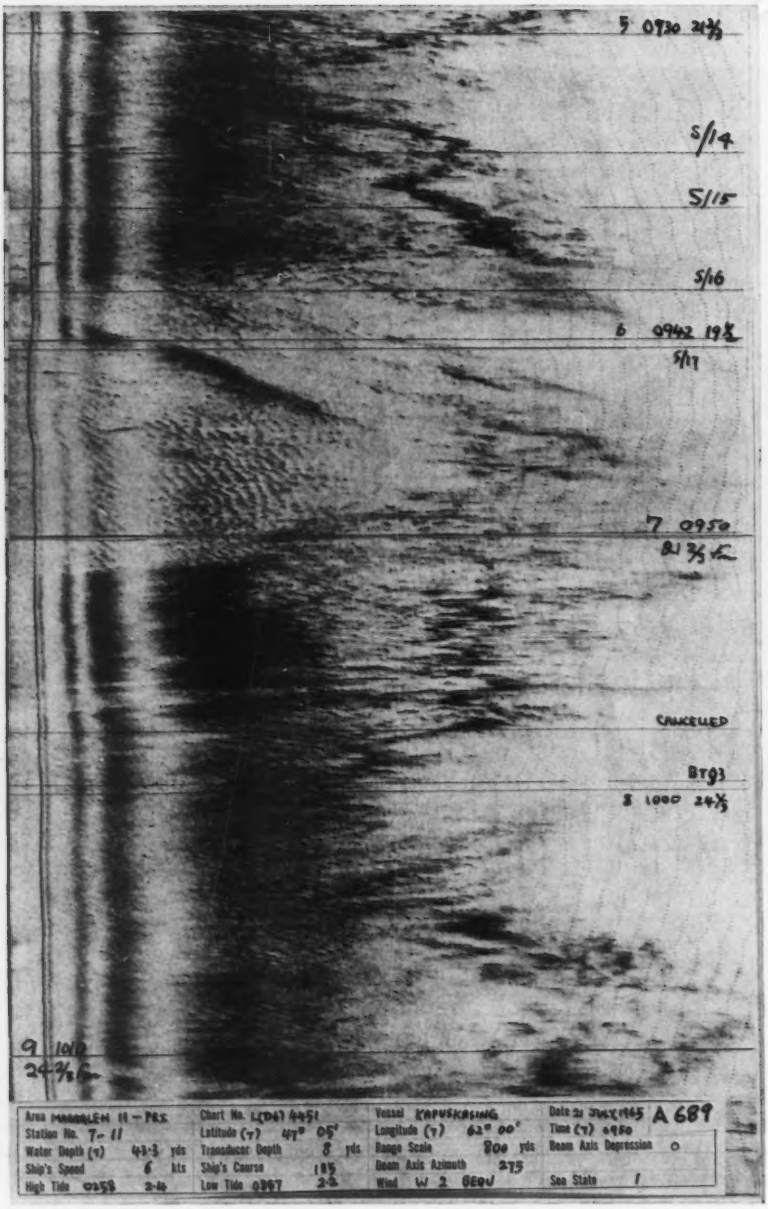

FIG. 4. Asdic record of about $4\frac{1}{2} \times \frac{1}{2}$ miles of sea floor between the Magdalen Islands and Prince Edward Island showing a rocky bottom (dark tones near marker line 5 and line 7) partially covered with a thin veneer of sediment (light tones between marker lines 6 and 7, and between lines 8 and 9). Small sand waves (approximately 1 ft high with a wavelength of about 10 yards) are indicated within the sediment-covered area by the light-toned wavy pattern between the marker lines 6 and 7.

FIG. 5. Bottom photograph representing an area of 1.64 m × 1.2 m at station S-75-25 (47°58′ N lat, 61° 38.4′ W long) some 13 miles north of the Magdalen Islands. The sandstone bedrock has only a thin cover of pebbles and rock fragments.

extending for distances of over 20 miles with only small local areas of somewhat irregular bottom relief, where bedrock controls the surface expression. Major irregularities occur where the sections cross the eastern Bradelle trough. The topography in this part of the shelf is generally smooth. This is produced by a nearly continuous cover of unconsolidated sediments over the sea floor. The sampling, asdic, and Sparker data suggest that the sediment cover is usually thin and probably varies between 0–10 m in thickness.

Bradelle Bank on the western part of the shelf, is an area of elevated bottom relief (minimum water depth about 25 fath) occupying some 200 square miles and elongated in a northwest–southeast direction (Fig. 1). It does not represent a moraine ridge or a ploughed up portion of the sea floor due to glacial scooping of soft sediments. Acoustical reflections (line 8) indicate that Bradelle Bank is a bedrock elevation on which there is a nearly continuous but relatively thin sediment cover. Near the edges of the bank, in somewhat deeper water, bottom samples and acoustical reflections indicate that the bedrock is at or very near to the surface of the sea floor.

On the shelf adjacent to the Laurentian Channel, north of the Magdalen Islands, the available echograms show that the sea floor slopes north with an average gradient of 18 ft/nautical mile towards the shelf break (see Fig. 3, line 15). The topography in this area has some depressions and highs. Pronounced topographic highs of 20–30 ft are found in water depths less than 80 ft. In water depths more than 80 ft, the relief of the sea floor has only minor irregularities. The topography in this area is not as rugged as that found to the south of the Islands but less smooth than that found to the west. It is an intermediate type when compared with southern and western parts of the shelf. The character of the relief in this northern part indicates that bedrock is at or near the surface of the sea floor. Samples and bottom photographs (Fig. 5) confirm this interpretation of the echograms.

East and southeast of the Magdalen Islands, the sea floor is smooth and forms a submarine terrace sloping to the east and southeast at an average gradient of 6 ft/nautical mile down to the 35-fath contour (see Fig. 3, line 18). The acoustical reflexions indicate a nearly continuous cover of unconsolidated sediments on the sea floor comparable to that found to the west of the Magdalen Islands. Further east, a major incisement (Cape Breton trough) occurs in the shelf (see Fig. 1). The western slope of this trough has an average gradient of 18 ft/nautical mile. The deepest part of the trough (110 fath) is near its mouth, adjacent to the Laurentian Channel. The eastern slope of the trough is steeper and has gradients varying between 50 and 300 ft/nautical mile. The bottom configuration of this incisement does not show the rugged relief encountered in the depression between the Magdalen Islands and Prince Edward Island. This is most probably due to the presence of a sediment cover on the slopes as well as in the centre of the trough. Southwards (Fig. 2) the trough narrows and decreases in depth towards the eastern end of the Northumberland Strait.

SEDIMENTS

The sampling program carried out on the shelf was designed to obtain a regional coverage. Hence, the locations of the sampling stations were based on a preliminary morphological map of the area rather than on an arbitrary grid system. Since sand- and gravel-size material is widespread in this area, most of the sampling was carried out with a modified Van Veen bottom grab. At suitable locations where finer-grained sediments occur, core samples were obtained. The following descriptions of the sediments are based on macroscopic examination of the samples. The system of nomenclature used is that of Nota (1958).

Sediments on the sea floor between Prince Edward Island and the Magdalen Islands are mostly composed of gravel- (particles >2 mm in diameter) and sand- (2–0.05 mm in diameter) size material. Gravel-size material is widespread and is mainly composed of reddish-brown friable sandstone of similar lithology to that found exposed along the north coast of Prince Edward Island. The sands are of coarse-to-medium-grain size (2.0–0.3 mm), and are mostly reddish-brown or brown except on the shelf near the Magdalen Islands where they are more brownish-gray. Locally, there is a quantity ($<30\%$) of pelite[5]-size (<0.05 mm) material mixed with the coarser-size grades. Samples containing pelite occur in the deeper and more protected parts of the sea floor; for example, very fine sand with an estimated pelite content of about 30% is found in the well-defined depressions (see Morphology of Shelf Around the Magdalen Islands).

Asdic records taken across the shelf between Prince Edward Island and the Magdalen Islands indicate that an almost continuous sediment cover occurs in the near-shore area of Prince Edward Island. Further offshore, the asdic records show frequent exposures of bedrock breaking through a thin discontinuous cover of unconsolidated sediments (see Fig. 4). Thus, the sediment pattern of the sea floor between Prince Edward Island and the Magdalen Islands can be described as a thin discontinuous cover of gravel- and sand-size material locally enriched with some pelite. These sediments lie on low dipping bedrock composed of reddish-brown friable sandstone similar in lithology to that exposed on the adjacent coasts.

West of the Magdalen Islands, sand-size material predominates where the sediment cover is thicker and more nearly continuous (Fig. 3). Although gravel-size material forms local concentrations, it is usually present only in small quantities. The sands are mostly gray and are of medium to fine-grain size (0.3–0.08 mm). Gravel-size material consists of sandstone bedrock and rocks (mostly igneous) foreign to the shelf area. The pelite content usually is low. A noticeable increase in the pelite content was found in such protected depressions as the Eastern Bradelle trough, where it forms a substantial admixture with the sands.

[5]The term pelite is used for material smaller than 0.05 mm in diameter.

On Bradelle Bank, a similar sediment pattern occurs. Most of the area is covered with medium- to fine-grained sand with local gravel fields. Near the edges of the bank, some bedrock exposures have been found. Asdic records obtained on Bradelle Bank confirm this sediment pattern. In addition, the asdic records show that sand waves occur in very localized sections of the Bank. Preliminary measurements indicate that the waves are several feet high and have a wavelength of 20–30 yards.

North and northwest of the Magdalen Islands on the shelf area adjacent to the Laurentian Channel, the bottom sediments consist mostly of gravel- and sand-size material. Pelite is almost completely lacking in the samples obtained from this area. Although pebbles of the local sandstone are abundant, rocks foreign to the shelf such as granites, gneisses, and basic igneous rocks occur in significant quantities. The percentage of sand in the samples is usually less than that of gravel. The sand present is of medium-grain size and is brownish-gray. Echograms show (see Morphology of Shelf Around the Magdalen Islands) a thin intermittent sediment cover with bedrock at or near the surface of the sea floor. The sediment pattern on this part of the shelf is best illustrated in Fig. 5, an underwater photograph taken at Station S-75-25 (47°58′N lat, 61°38.4′W long) some 13 miles north of the Magdalen Islands in 180 ft of water.

East and southeast of the Magdalen Islands, the sea floor is covered with sand mixed with varying quantities of pelite. The percentage of pelite in the samples increases with increasing water depths towards the Cape Breton trough while the sand becomes finer grained. Below about the 45-fath contour, the pelite component becomes the predominant grade size and the sand is fine grained . Cores collected in the centre of the trough show distinctly a twofold zonation. The top layer, a few centimeters thick, is brownish while the underlying materials are dark gray. The top layer is composed of a soft pelite containing some gravel and sand while the lower layer is a relatively stiff pelite in which only occasional pebbles are found. Sub-bottom reflections recorded by the echosounder in the central parts of the trough indicate a change in the lithology of the sediments of about 10 ft below the surface of the sea floor. Cores taken at this area, however, failed to penetrate to this depth. Sand and gravel comprise the bottom sediment close to the coast of Cape Breton Island in water depths less than 20 fath. The acoustical and sampling data indicate that there is nearly continuous sediment cover in the shelf area east and southeast of the Magdalen Islands and in the Cape Breton trough.

CONCLUSIONS

The tentative conclusions based on the geomorphological reconnaissance of the shelf throughout the southern Gulf of St. Lawrence are:

The major morphological characteristics of the shelf are not the product of present environmental conditions. Instead, the shelf, usually referred to as the Magdalen Shallows, bears the marks of an extensive Pleistocene glaciation. The submarine troughs (of which Chaleur Bay and the Cape Breton troughs

are the most conspicuous) and the tunnel valleys (south and west of the Magdalen Islands) are ample morphological evidence of glaciation.

The submarine platform around the Magdalen Islands is a gently sloping floor of Palaeozoic bedrock with a thin cover of unconsolidated sediments which is interrupted in places where the bedrock protrudes. The unconsolidated sediments are believed to be mainly the erosional products of a former larger elevated area of which the present archipelago of the Magdalen Islands is a small remnant. Such erosion products fail to cover large areas of the shelf between the Magdalen Islands and Prince Edward Island.

The Pleistocene ice sheets must have met a dissected land area developed in nearly horizontally layered rocks of which Bradelle Bank, Orphan Bank, and some unnamed banks represent the remnants of mesa-like bedrock elevations. The present trough-shaped submarine valleys must have formed part of the major channels of the drainage system developed on the substratum of low dipping bedrock.

During Pleistocene glaciation the entire shelf was presumably covered with ice sheets. The ice invaded the area with lobes through the main channels of the pre-Pleistocene drainage system, and modified the channels into the present submarine troughs. Presumably the ice spread out over the remainder of the shelf, although it failed to modify more than the details of the relief with the exception of the formation of tunnel valleys. There are no indications that the activity of the Pleistocene ice has left major depositional features on the areas of low relief.

The postglacial transgression probably modified the Pleistocene morphology and caused some marine planation. One indication of this is given by the broad terrace between approximately 28 and 34 fath, which is well developed around the Magdalen Islands but less pronounced off Prince Edward Island. This terrace probably marks a former shoreline resulting from a standstill in the postglacial transgression.

ACKNOWLEDGMENTS

The authors wish to thank Professor D. J. Doeglas, Professor G. C. Maarleveld, State Agricultural University, Wageningen, Holland, Dr A. H. Bouma, University of Utrecht, Dr D. J. Stanley, Dalhousie University, for their interest and constructive comments on the manuscript. They are indebted to Professor D. Chesterman and his assistant Mr Kim Wong of Hong Kong University, for their demonstration of the Kelvin and Hughes and subhorizontal asdic equipment under the auspices of the Marine Sciences Branch of the Canada Department of Mines and Technical Surveys. The authors were assisted in the field by Mr R. J. Lahey and the technical staff of the Atlantic Oceanographic Group and the officers and men of CNAV *Sackville* and CSS *Kapuskasing*, and the preparation of the illustrations by Messrs G. Buurmen and Z. Van Druuten.

The second author would like to express his appreciation to Dr F. R. Hayes, Chairman of the Fisheries Research Board of Canada, and to Dr R. W. Trites of the Atlantic Oceanographic Group, for the invitation to participate during employment in the summer of 1965, in the field work on the submarine geology of the southern Gulf of St. Lawrence.

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Food and Growth of Fishes.
III. Relations Among Food, Body Size, and Growth Efficiency[1]

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ABSTRACT

Reexamination of published data on growth and feeding of fishes shows that when fish are fed on one type of food, the logarithm of the gross growth efficiency (log K) decreases with increase in rations. For a number of species and experimental situations this relation is adequately described by the linear equation

$$\log K = \log (\Delta W/R\Delta t) = -a - bR$$

whence

$$\Delta W/\Delta t = Re^{-a-bR}$$

where ΔW is the growth, R the rations intake during the period of time Δt, and a and b are the parameters fitted to the linear form of the equation. With a single food-supply level, rations are highly correlated with body weight so that either one may be used to predict the growth efficiency. However, comparison with experimental situations which induce changes in rations intake at given body size, suggests that body size is not the determining factor as long as environmental conditions are within the normal biokinetic range. That is, the basic pattern of distribution within the animals of the energy intake is described by a knowledge of the rate of intake and two parameters.

The action of various environmental factors appears to be reflected in this equation in different ways. In the experiments examined changes in temperature, which are known to affect the level of total metabolism, affected the value of R but the parameters a and b remained unchanged. That is, temperature changes appeared to affect only the energy turnover rate, not the distribution of energy in the fish. By contrast, changes in factors such as salinity and metabolic wastes, which are known to affect the metabolic load, affected the values of a and b, and showed interaction with body-size as well. The factor having the most important influence on the parameters seemed to be the type of food, especially with respect to particle-size. We infer that this simple effect on the linear equation is a characteristic expression of the complex integration of expenditures during searching and grazing with the success of this activity.

These observations imply that the growth efficiency equation, or what we term K-line, provides a useful index of the costs of particular behaviour patterns in particular ecological situations. Together with observations on metabolic rates it may also be used to describe the growth of fishes in relation to their food supplies. It is thus a potential indicator of the relative positions of life-history phases of various species in the production system represented by a natural community.

INTRODUCTION

Growth is an expression of the operation of the energy system in the animal. Hence, in individual fishes, study of growth as a facet of biological production

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J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

processes requires that it be related to the energy supply or food intake, the energy dissipation or total metabolism, and the circumstances under which the energy exchange takes place. For an individual this system may be represented by the descriptive equation

$$pR = T + \Delta W/\Delta t \tag{1}$$

where R is the food consumed, T is the metabolism, $\Delta W/\Delta t$ is the growth rate, and p a term for correction of consumed ration to physiologically useful ration and conversion of the various measures to common energy units. The study of growth processes thus implies specification of the functional relations among these elements.

In an earlier paper (Paloheimo and Dickie, 1966) we pointed out that for a given level of availability of food the energy system appears to be homeostatically regulated in such a fashion that in fish of different sizes the value of pR results in a value of T which can be predicted from the body weight W. That is, in the expression

$$T = \alpha W^{\gamma} \tag{2}$$

the value of γ appears to be constant, while values for α reflect particular conditions of food supply and temperature as mediated by R, T, and W. Such regulation of the relation between R and T implies that there may be similarly predictable relationships between R or T and the remainder of the energy system, $\Delta W/\Delta t$, a phenomenon also suggested by reported observations of regular patterns in growth curves of $\Delta W/\Delta t$ against W or time.

In this paper we reexamine data from several published experiments which have observed food consumption and growth under different conditions. The results suggest that it is possible to describe general relations between growth and energy intake in a form which is somewhat simpler than has been thought heretofore. In the discussion we suggest that, if this proves to be generally true, the system of equations which describes the relationships provides a basis for further experimental and field investigation of the role of the interactions of fish and their food in natural production.

METHODS OF STUDYING GROWTH EFFICIENCY

Different methods have been proposed for studying the relationship between growth rate, $\Delta W/\Delta t$, and the rations, R, or metabolism, T. Ivlev (1945) reviewing earlier concepts and definition of terms, proposed, among other possibilities, the study of growth efficiency in the form of the simple ratios:

$$K_1 = \frac{\Delta W}{R\Delta t} \text{ or } K_2 = \frac{\Delta W}{pR\Delta t}$$

depending on whether an index of the total consumed ration, R, or the energy equivalents of the physiologically "useful" ration, pR, were used. Some of

the problems involved in deriving appropriate energy conversion values for p were discussed briefly in our earlier paper cited above. Of particular importance is the detection of possible changes in p with time, place, food, and fish-flesh constitution.

Attempts have been made to study growth phenomena in more detail than implied by the ratios K_1 or K_2. One approach has been to isolate various dietary constituents and study them separately. Particular interest has centred on nitrogen equivalents of food and growth because of their apparently direct relation to protein structure of the animal body.

Unfortunately, attempts at corrections of field observations for secular changes in nitrogen content of food and fish flesh appear often to have introduced errors comparable in size to the differences they were designed to eliminate (Winberg, 1956). Difficulties also arise in the interpretation of laboratory studies of utilization of nitrogen, such as reported by Gerking (1952, 1955). He found that his index of K_2 for nitrogen metabolism increased with amount consumed. However, his data indicate that the gross efficiency of overall food used, K_1, reviewed in more detail later in this paper, showed the opposite trend. His data also show that the proportion of N_2 in the food used in his experiment was initially lower than it was in the fish flesh, and that during the experiments the relative N_2 of the fish flesh decreased, larger decreases being associated with larger food consumptions. Thus, his results for N_2 appear to reflect a transitional rather than a balanced state of the body constituents. Brown (1951) demonstrated that during "transition states" of feeding on deficient or potentially toxic diets, overall growth of trout may be normal for several weeks, even although prolonged feeding on the diet eventually leads to abnormal growth, pathological symptoms, and even death. It thus appears that during various growth periods utilization of particular food and body constituents may show changes or trends which are different from changes in the total energy exchange. Separate examination of body and food constituents may, therefore, be essential for understanding certain aspects of growth and growth efficiency. However, as was implied by the early work of Titcomb et al. (1929), significance of changes in the constituents may be difficult to judge without concomitant information on the gross changes. The fates of the separate constituents are not necessarily reliable indices of the operation of the total energy system.

An alternative to the study of dietary fragments has been the study of metabolic fractions. Thus, attempts have been made to define a basal or maintenance fraction of metabolism which can be measured and subtracted from the total, permitting study of net growth efficiency. This maintenance fraction has been defined in different ways. Dawes (1930a, b) and Pentelow (1939) defined it as the energy equivalent of average rations consumed per unit time during a prolonged period of no growth. Ivlev (1960, 1962), von Bertalanffy (1938, 1964) and Smith (1963) define it as the rate of dissipation of stored body substances (N_2 equivalents) during starvation. However, Brown (1946b)

observed that there are oscillations in the efficiency of utilization of food for weight growth, apparently related to deviations from an average "condition" factor for the fish body. Hence, subtraction of an average value for maintenance from independently observed total metabolic measures may introduce relatively large errors in calculated net efficiency, making detection of general patterns unnecessarily difficult. Brown (1957) noted that in some cases the net efficiency calculated in this way may be more than 100%. In addition Brown (1946b) found that the amount of food required to maintain a given weight depended upon the feeding rate to which the fish was previously accustomed. She thus defined a maintenance requirement as the minimum food level to which fish could be acclimated to maintain constant weight: a definition which is different from either of the two definitions given below. Beamish (1964) found that because of differences in voluntary activity, routine energy expenditure was quite different at different levels of starvation. Compensatory increases in growth following starvation due to deficient diet (McCay et al., 1929) or to injury (Weiss and Kavanau, 1957) have long been recognized.

In the face of such varied opinions and findings we can only conclude that while definition of fragments of the energy system has a logical appeal, the interpretations of the particular definitions are of questionable significance, and the technical difficulties of measuring and calculating the quantities that support them could lead to erroneous formulations. The further conceptual complexities of extrapolation from equilibrium conditions of "maintenance" to actively growing states were emphasized by Brody (1945).

Our study of metabolic relations of fishes (Paloheimo and Dickie, 1966) suggested that it is the total metabolism of fishes, rather than some readily identifiable fraction of it, which underlies regulation of the energy system. This, together with the difficulties encountered above in fragmentation of the energy system, either in terms of diet constituents or metabolic fractions, suggests that at least initially there is good reason to study gross energy relations in the simple form suggested by Ivlev. In what follows, we have therefore calculated growth efficiency in the form of K_1. In studying its relation to the remainder of the energy system, we have, furthermore, used the logarithm of the growth efficiency. This form was adopted partly because, as will be shown later, it appeared to be linearly related to other variables such as rations and body weight. But this form has the added advantage that $\log K_1$ differs from $\log K_2$ only by a constant amount equal to $\log p$. Hence, uncertainty about actual values of p affects only the position or intercept of a line relating $\log K$ to the other variables, and does not affect its slope as long as p remains constant. Under such circumstances it seemed preferable to use K_1 (in the sequel denoted simply K) rather than K_2 and hence avoid assigning arbitrary values to p where the analysis can be carried out without them. Interpretations of the resulting intercept of the gross growth efficiency lines may be made separately where there is appropriate experimental information.

FACTORS AFFECTING GROWTH EFFICIENCY

The literature on food and growth of fishes contains numerous references to growth efficiency and factors which may affect it. However, such potentially important variables as body weight, age, food consumption, and temperature are so frequently confounded in experimental designs that it is difficult to separate their effects. Thus, it is generally accepted that growth efficiency is high in the yolk sac and very young stages and decreases thereafter, depending on a number of factors. Ivlev (1945) states that in all aquatic organisms age is the most important factor, although as pointed out by Ricker (1946) this appears based on experimental observations on invertebrates rather than fish. Age was similarly regarded as important by Gerking (1952) and Kinne (1960) from their studies. However, they appear to treat age as a general term comprehending trends in a number of factors such as increases in body size and food consumption, any one of which may have been related to downward trends in growth efficiency. Their analyses do not seem to have been designed to measure effects of such variables separately. Kleiber (1947, 1961), on the basis of work with warm-blooded domestic animals, seems to have been the first to conclude that utilization of food for production processes, including growth, is independent of body size. While we do not know of specific attempts to verify this with fishes, its acceptance seems implied by the interpretations of Ivlev, Gerking, and Kinne.

Brown (1957) reviewing her own and other work, stressed the importance of the level of feeding. Thus, while she found temporal differences in appetite and growth efficiency, differences due to position in social hierarchies, and type of food, she concluded that individuals showed characteristic appetites, higher intakes being associated with lower growth efficiencies. She also concluded that within individuals the efficiency of conversion of food to fish flesh was highest at near maintenance levels, decreasing with increases in the amount fed, supporting a similar suggestion of Dawes (1930a, b). Despite the high temporal and individual variability in the data available to her, she concluded that food supply is probably the most "potent" factor affecting growth.

Brown (1957) regarded such physical environmental variables as temperature to have an important influence on growth only through their effects on food requirements and rates of feeding. In salmon embryos, Hayes and Pelluet (1945) found that above a minimum of 7 C, efficiency of conversion of yolk to embryo flesh was positively correlated with temperture. In fish past the yolk-sac stage, Winberg (1956), citing his own and earlier Russian literature, concluded that temperature had virtually no effect. However, Kinne noted appreciable differences in growth efficiency at various temperatures and salinities and found that the resulting growth tended to be highest at intermediate values of both. Complicated interactions of growth with at least temperature are perhaps to be expected, in view of observations such as those of Wingfield (1940) who noted rather different growths at the same temperatures in ascending and descending temperatures series. Similar effects of temperature on metabolism are well known (Fry, 1947; Job, 1955) and inter-

actions with temperatures and food supply were noted in our review (Paloheimo and Dickie, 1966) of metabolic relations derived from food–growth experiments.

It thus appears that there is a considerable body of experimental data which provides information on factors affecting growth and growth efficiency. In view of the apparently high variability within individuals at different times, possible interactions of the main variables, coupled with technical difficulties in maintaining constant conditions, to say nothing of difficulties in defining appropriate measures of growth efficiencies, it is not surprising that there have been difficulties in generalizing the results of particular experiments. However, a number of these have now been reported in sufficient detail to permit statistical analyses. In what follows we report our reanalyses of the data which are available to us in the literature. The results, taken together, appear to verify conclusions reached by earlier workers with respect to the importance of food supply and temperature. What is perhaps more important for present purposes is that they support the suggestion from our metabolic studies that there may be a basic conservatism in the pattern of food–growth relations which would permit us to characterize and study it in more specific form.

REANALYSES OF PUBLISHED EXPERIMENTAL DATA

Dawes' Plaice Experiments

A number of the food consumption and growth experiments reported by Dawes (1930a, b) were carried out on individual 2-year-old European plaice (*Pleuronectes platessa*) fed on a single type of food (chunks of the common mussel, *Mytilus edulis*). Fish were held at two different localities in wire cage compartments on large floats. Individuals were introduced into the cages at different times and any one which died was replaced by another, usually of similar size. Food was administered at two rates above the maintenance level, although only four individuals were fed an "intermediate" ration. The rest, numbering about 50 fish, were fed *ad libitum* or maximum rations; that is, excess food was kept in the cages at all times. Observations of growth in weight and length, and food consumption of each individual, all at approximately 2-week intervals are reported in extensive tables. Separate charts of biweekly average temperatures were also provided. Data are thus available for examining relations between growth efficiency, rations, body weight, temperature, and condition factor.

Using the data for intermediate and maximum feeding rates[3] we have calculated the log gross growth efficiency, i.e. $\log K = \log (\Delta W/R\Delta t)$, from the data on growth in wet body weight and the wet weight of the mussel food, since no dry weight or caloric determinations were made.

Our metabolic studies of these same data (Paloheimo and Dickie, 1966) showed a marked difference in the relation of metabolism to body size in the

[3]In compiling these data we have excluded those observations made in the month preceding death of all fishes which died during the course of the experiments.

ascending and descending phases of the seasonal temperature changes during the experiments. In this analysis of food–growth relations we have accordingly separated the data into an ascending and descending temperature series as described earlier, and carried out the statistical analyses for each series separately. Since we could find no statistically significant differences in food, growth, or metabolic relations between sexes, the data for sexes were combined. Similarly, differences between localities seemed indistinguishable from differences in season or size of fish, and these data were combined as well. The principal results of the analysis are summarized in Table I.

The upper parts of Table I contain a series of simple correlations among the logarithmic growth efficiency, log K, and ration, R, initial body weight, W, and average temperature, $t°$. K and R have been corrected to a standard 2-week period. Also shown are a series of partial correlations with log K, corresponding with the simple comparisons, but eliminating the estimated linear effect of one of the other two variables. In the bottom part of the table we give overall correlation coefficients, and partial slopes of multiple regression of log K on R and on W, when W or R as well as $t°$ are held constant.

Each of these analyses was first carried out on the overall data; that is, without distinguishing between observations for different individuals. Secondly, we have carried out a covariance analysis within individuals. A third analysis was carried out using the means for individuals.

Noting the experience of Brown (1946b) that growth efficiency was related to condition factor in the brown trout, we also included condition factor as an additional variable in our analyses. That is, defining condition factor as

$$q = W/L^n$$

we determined an overall value for n from the slope of the regression of log W (weight) on log L (length) from all the data. A value of q was then calculated for the beginning of each observation period from the observed initial W and L, using this average value for n. The analysis indicated that in no case did condition factor derived in this fashion have a significant effect on the utilization of food for growth during the following 2-week period. However, condition factor was highly correlated with the body weight, being generally low when an experimental animal was first placed in the cages, and increasing rather rapidly to a more or less constant value after about 6 weeks as the fish grew. Because of this confounding, it cannot be concluded that the body condition, q, is of negligible importance in the growth of plaice, but only that it could not be studied from Dawes' experimental design. Correlation coefficients involving it indicated nonsignificant effects throughout and have therefore been omitted from the already complicated table.

As was expected from our metabolic studies, correlation and regression coefficients for the overall data appear from Table I to be quite different in the ascending and descending temperature series. Correlations in the ascending temperature series show a low but significantly negative simple correlation

TABLE I. Results of reanalysis of Dawes data on feeding and growth of plaice to show effects $\Delta W/R\Delta t$, where $\Delta W/\Delta t$ = wet body weight growth per unit time, R = wet weight

		Ascending temperature series								
			Overall temperatures						Within temperatures	
		n	log K,R	log K,W	log K,$t°$	R,W	R,$t°$		log K,R	log K,W
Overall data										
Simple correlations		202	−.25**	−.22**	−.11	+.45*	+.50**		−.16*	−.16*
	/R			−.12	+.02					−.10
Partial correlations	/W		−.18*		−.15*				−.09	
	/$t°$		−.23**	−.24**						
Within individuals										
Simple correlations		202	−.04	−.28**	−.12	+.51**	+.30*			
	/R			−.30**	−.12					
Partial correlations	/W		+.13		+.04					
	/$t°$		0	−.25**						
Individual means										
Simple correlations		52	−.42**	−.26	−.14	+.45*	+.54*			
	/R			−.10	+.12					
Partial correlations	/W		−.35**		−.20					
	/$t°$		−.41**	−.30*						

	Overall correlation coefficient		Partial slopes	
	n	R	$b_{\log K,R/W,t°}$	$b_{\log K,W/R,t°}$
Overall data	202	.28**	−.0022 ± .0029	−.0019 ± .0020
Within individual	202	.30**	+.0038 ± .0048	−.0124 ± .0069
means	52	.43**	−.0049 ± .0046	−.0002 ± .0030

**Exceeds value expected at the 1% probability level.
*Exceeds value expected at the 5% probability level but less than 1% level.

of various factors on the logarithm of the gross growth efficiency, log K. K is calculated as of consumed rations. Other symbols: W = wet body weight, $t°$ = temperature in C.

Descending temperature series

	Overall temperatures					Within temperatures	
n	log K,R	log K,W	log K,$t°$	R,W	R,$t°$	log K,R	log K,W
228	+.17*	+.01	−.08	+.63**	+.25*	+.17	+.06
		−.13	+.04				−.11
	+.21**		+.09			+.20*	
	+.15*	+.04					
228	+.16*	−.25**	+.13	−.28**	+.52**		
		−.22**	+.06				
	−.10		−.14				
	+.11	−.26**					
44	+.25	+.21	−.17	+.81**	0		
		+.02	−.22				
	+.13		−.15				
	+.28	+.20					

n	Overall correlation coefficient R	Partial slopes $b_{\log K,R/W,t°}$	$b_{\log K,W/R,t°}$
228	.22**	+.0043 ± .0026	−.0021 ± .0020
228	.35**	+.0067 ± .0047	−.0116 ± .0053
44	.32*	+.0026 ± .0037	−.0005 ± .0028

between log K (growth efficiency) and both R (rations), and W (body weight). The partial correlations show that the relationship with R is slightly weakened when the linear effect of differences in W is removed. But when we correct for differences in R the inverse correlation with W becomes insignificant. Corrections for $t°$ (temperature) had no apparent effect. By contrast, in the descending temperature series log K shows a low but positive simple correlation with R, although there was no significant relation to W. The relation with R is slightly strengthened when effects of W are removed as shown by the partial correlation coefficients. The effects of $t°$ again appear negligible. These seemingly relatively minor effects of temperature within temperature series showed up again in a covariance analysis within 1 C temperature strata. The smaller range of variables within strata is undoubtedly responsible for a (observed) lowering of the correlation coefficients, which are, however, not otherwise affected.

In our metabolic studies (Paloheimo and Dickie, 1966) we concluded that differences in relations between the ascending and descending temperature series for the overall data may have resulted from complex interactions involving temperature acclimation phenomena as well as the nonbalanced distribution of individuals of different sizes in the two parts of the seasonal temperature range. Growth efficiency seems to be similarly affected. In addition, the confounding of growth, rations, body weight, and temperature in the ascending series, and of growth, rations, and temperature in the descending series makes separate appreciation of their effects virtually impossible from the data in this form. Some of the difficulties in interpretation are resolved when we consider the data by individuals in the next section of Table I. The results of the covariance analysis within individuals are given in the second section of the table, and of individual means in the third section.

In the ascending temperature series there is within individuals a strong positive simple correlation between R and W. However, during the growth of individuals on a constant food supply, changes in body weight are generally proportionately larger than changes in rations. In keeping with this the data within the individual plaice show a rather larger negative simple correlation of log K with W (−0.28) than with R (−0.04). Similarly, there is a highly significant negative partial correlation between log K and W eliminating R (−0.30), but when W is eliminated the partial correlation between log K and R remains insignificant. Such effects are to be expected from a study of the growth of individuals at a given level of feeding.

Comparisons of the mean responses of different individuals provides a contrast with this situation. That is, the calculation of averages for individuals tends to minimize the body-size range. The plaice were, in fact, deliberately chosen to be of near uniform group starting sizes. The method of analysis by individual means thus emphasizes the effect associated with differences among the appetites of individuals. The result in the third section of the table, showing a strong negative partial correlation of log K with R but weak correlation with W is therefore evidence for the primacy of the influence of the ration

on growth efficiency. The contrast between results within and between individuals with the bulk of data coming from a single feeding level, suggests that within individuals the importance of the ration was obscured by the confounding with body weight.

Similar effects may be partly distinguished in the descending temperature series, where, however, we also obtain a hint that temperature within the series may be more important than emerged before. Thus, within individuals in the descending temperature there is an inverse correlation between R and W, which appears to have been associated with the fact that most fish continued to grow, but their food intakes decreased with the decreases in temperature. There is, furthermore, a low but positive correlation between log K, and $t°$ suggesting that those fish which maintained their appetite did relatively better than those which lost their appetite. The former were evidently the smaller fish, since the simple correlation between log K and W is strongly negative. By contrast, the correlation between R and W for individuals means was strongly positive in the descending temperature series, despite the decreasing temperatures and falling appetites within individuals. This may account for the fact that with data on only 44 fish none of the remaining relations among individual means were strong enough to be distinguished from random variations. While the main effects shown in the descending temperature series are thus similar to those found in the ascending series, it appears from the side effects that important interactions with temperature may be involved, but were not evident during the ascending temperature phase, possibly because of complete confounding with other variables.

The effects of this interaction with temperature are reflected again in the partial regression coefficients given in the bottom panel of Table I, where although the main effects for both the ascending and descending temperature series are the same as shown by the simple analysis, and the overall regression coefficients are generally significant at the 1% level, neither R nor W is a sufficient predictor of log K when the effects of $t°$ are eliminated at the same time. An exception to this is the strong negative partial regression between log K and W within individuals ($b_{\log K,W/R,t°}$).

In addition to his experiments with individual fish, Dawes (1930a) reports four preliminary experiments with groups of four to six fish of similar size. Two groups were fed maximum rations and two intermediate rations. Unfortunately, there were too few points available to permit analysis of a separate ascending series. However, the descending series showed significant negative simple and partial correlations of log K with both R and W, overall and within rations levels. This result is the same as was obtained above from the analysis for individuals in the ascending temperatures, but is the opposite of that shown in the descending series. Such a reversal of effects serves to emphasize the likelihood that it is the design of the experiments, particularly with respect to the seasonal periods for which fish of various sizes were held in the temperature series, that has introduced much of the difficulty into interpretation of the results.

The main impression left by this reanalysis of the plaice data is one of high variability in growth efficiency in relation to the other observed variables. However, the correlation and regression coefficients are strong enough to demonstrate that the relationships exposed are unlikely to have been fortuitous. In fact, despite the high variability and confounding, our findings support those of Brown that, at least in the ascending temperatures, food intake is of first importance in determining relative growth efficiency, the higher intakes being used less efficiently. Apparent contradictory results between ascending and descending temperatures may be partly attributed to the fact that highest experimental temperatures were on the fringes of the biokinetic range of the larger fish. In nature, it is unlikely that they would ever be found at these high temperatures (20–22 C). Within individuals, the strong inverse correlation with body weight does not necessarily contradict Kleiber's (1947) generalization, since it appears associated with the relations among body size, food intake, and temperature when there is only one rate of food supply. Further clarification and specification of these relationships appears possible only by reference to experiments designed to separate and test them under different conditions of food supply.

Pentelow's Brown Trout Experiment

An analysis similar to that for the plaice data was carried out on the data for brown trout reported by Pentelow (1939). He held individual trout in separate compartments of tanks at ambient water temperatures for periods ranging from a few weeks to nearly 2 years. In addition to a maintenance feeding regime, results of which were discussed in connection with our metabolism studies, he fed nine fish on an *ad libitum* diet of live *Gammarus* and reported body weights, food consumptions, and average temperatures for observation periods of from 2 to 7 weeks. We have again calculated log K from the ratio of wet weight of fish growth and food consumptions, and studied its relation to calculated food consumed per standard 2-week period, initial body weights and average temperatures in ascending and descending temperature series. The results are shown in Table II with a layout similar to that of Table I.

The results from the overall data showed a high simple negative correlation of log K with both R and W in both the ascending and descending temperature series. The same though stronger simple correlations were shown by the covariance analysis within individuals. With data for only nine individuals, there were no statistically significant relations detectable for individual means. The agreement in the relations in the two temperature series is in keeping with results of our earlier study of metabolic relations, based on the same data. They revealed no detectable differences in the relationship between metabolism and body size in the ascending and descending temperature series. In conjunction with the plaice data this suggests that any differences between ascending and descending temperature series are likely to be reflected in both the metabolic and growth components of the energy system.

TABLE II. Reanalysis of Pentelow trout data — relations among log growth efficiency, rations, body weight, and temperature (see legend of Table I).

		Ascending temperature series						Descending temperature series					
		n	log K,R	log K,W	log K,t°	R,W	R,t°	n	log K,R	log K,W	log K,t°	R,W	R,t°
Overall data													
Simple correlations		40	−.31*	−.41**	−.26	+.85**	+.49**	34	−.36*	−.28	−.49**	+.49**	+.53**
Partial correlations	/R			−.30	−.14					+.19	−.38*		
	/W		+.09		−.22		+.69**		−.30		−.43**		+.58**
	/t°		−.21	−.39*		+.90**			−.13	−.12		+.95**	
Within individuals													
Simple correlations		40	−.41**	−.42**	−.31*	+.87**	+.53*	34	−.42**	−.36*	−.64**	+.93**	+.51**
Partial correlations	/R			−.14	−.12					+.13	−.54**		
	/W		−.10		−.26		+.76**		−.28		−.59**		+.57**
	/t°		−.30	−.38*		+.93**			−.14	−.18		+.94**	
Individual means													
Simple correlations		7	−.05	−.39	−.14	+.86*	+.33	8	−.13	−.01	−.02	+.96**	+.55
Partial correlations	/R			−.70	−.13					+.43	+.07		
	/W		+.63		−.11		+.52		−.45		−.02		+.59
	/t°		.00	−.39		+.89*			−.15	.00		+.96*	

**Exceeds value expected at the 1% probability level.
*Exceeds value expected at the 5% probability level less than 1% level.

The calculation of the partial correlation coefficients from the trout data showed one important difference from the effects shown by the plaice data. In the brown trout data, the partial correlations of log K with both R and W were reduced appreciably when adjustments were made for differences in $t°$. This suggests that temperature was an important source of variability among the observations more clearly than could be discerned from the plaice studies. Unfortunately, with only one feeding level, the temperature, rations, and body size changes were again confounded in the experiments, making it impossible to assess the importance of any one of them alone from the observations.

Hatanaka's Plaice Experiments

Limanda yokohamae

The experiments described by Hatanaka et al. (1956a) on the Japanese plaice, *Limanda yokohamae*, were carried out at ambient temperatures and are similar to those of Dawes, except that the fish were reared together in a large tank and the total observation periods were short : from 10 days to a month, after a 15-day acclimation period in the tank. This short period of observation precluded long temperature trends of the sort which occurred during the experiments of Dawes and Pentelow, although the previous temperature history of the fish may still have influenced the results. Only initial and final weights and total food consumptions are given for each individual but three initial size groups of fish were used, ranging in age from 0 to 3-year-olds.

The food used in the experiments was whole marine annelids of various sizes. Earlier observations had shown that they are one of the major components of the natural diet of these plaice in the Bay of Sendai. The feeding system may be considered as "restricted" in the sense that all the fish were fed to satiation once a day rather than being supplied with excess food at all times. The individuals were tagged and records kept of the food consumption of each individual, as well as its total growth during the experiment. Three experiments were conducted at different seasons, hereafter referred to as three different temperatures (averages: 8.4, 13.1, 19.0 C).

From the data which give both wet weights and caloric equivalents we have calculated log K for individuals and averages for initial size groups (<100, 101–200, $>$ 200 g) in terms of caloric equivalents, and calculated simple and multiple correlation and regression coefficients for its relation to R in calories as well as to W as wet body weights, both for individual fish and for the means for size groups, overall and within temperatures.

As expected from the high variability revealed by our metabolic studies, and the experience of Brown and Dawes, growth efficiencies for individuals showed high variability. There was an overall significant negative correlation between log K and W, but the overall correlation coefficient for combined effects of R and W accounted for only about 25% of the total variation. The correction for temperature groups was insignificant.

When averages for the initial size groups (different from the size groupings discussed by Hatanaka) were used, most of this scatter was removed, the multiple regression accounting for over 90% of the variation (i.e. $R^2 > 0.90$). The results of the analysis using means of size groups are summarized in Table III. It shows in the first column that the simple negative correlation between log K and R (−.84) is high, but not as high as that between log K and W (−.94). This, together with the high simple positive correlation between R and W, results in partial correlations shown in the third column, which assign the changes in log K entirely to the changes in W, the partial correlation with rations (+.41) being insignificant at the 5% level. Covariance analysis within temperature groups showed that the temperature (i.e. seasonal) effect was not significant, although, as shown by columns two and four of Table III, the correlations were generally higher when adjustment was made for mean differences among the temperature series.

TABLE III. Correlation coefficients, **r** and **R**, between log growth efficiency (log K), rations (R), and body weight (W) in the plaice, *Limanda yokohamae*. The 49 observations on individuals were grouped into three different initial size groups of the plaice (see text) at two different temperatures, and two of the size groups at a third temperature (data from Hatanaka et al., 1956a).

	Simple correlations			Partial correlations	
	Size group means overall temperatures	Size group means within temperatures		Size group means overall temperatures	Size group means within temperatures
$r_{\log K,R}$	−0.84**	−0.92**	**R**	0.95**	0.98**
$r_{\log K,W}$	−0.94**	−0.98**	$r_{\log K,R/W}$	+0.41	+0.43
$r_{R,W}$	+0.94**	+0.96**	$r_{\log K,W/R}$	−0.84**	−0.91**

**Significant at the 1% probability level.

The log mean growth efficiency (in calories) for the size groups within temperatures is plotted in Fig. 1, in relation to rations (in calories) and body weights (grams). From Table III and Fig. 1 it is clear that either the rations or the body weight could be used to predict the growth efficiency change. However, as with the Dawes plaice data, within the one feeding regime the range of initial body weights was greater than the range of rations intakes. This persistent relation throughout the experimental results is reminiscent of the recognized relations between body size and metabolism which show that larger fish have a lower metabolic rate. However, from these data it appears in addition that not only does the rate of rations intake decrease with increase in size, but that it apparently decreases at a faster rate than does the respiratory metabolism. The result is that with increasing fish sizes,

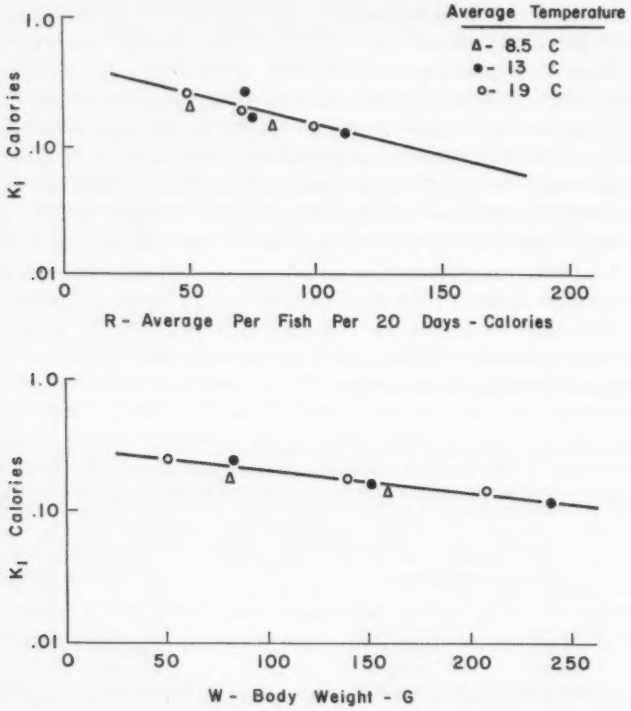

FIG. 1. The relation between the logarithm of the gross growth efficiency log $K_1 = \log \Delta W/R\Delta t$ ($\Delta W/\Delta t$ = growth rate; R = rations) and the rations and initial body weight, W, in the Japanese plaice, *Limanda yokohamae* (Hatanaka et al., 1956a). Plotted points are means for groups of fish of similar initial weights. The food was whole annelids.

smaller and smaller proportions of the increasing total energy intake were channelled into growth. This general effect has, of course, long been recognized. The contribution made to our understanding by analysis of these data is the recognition of a possibly simple relationship among the variables; Fig. 1 indicates that log K decreases linearly with increasing R or W. Unfortunately, since again only one rate of feeding was studied, we cannot establish whether the efficiency change observed in these experiments applies over all rations and weight levels, or is peculiar to this one feeding level.

KAREIUS BICOLORATUS

A series of experiments similar to those on *L. yokohamae* were carried out on *Kareius bicoloratus* (Hatanaka et al., 1956b) to examine the effect of different diets. The experiments on 32 individuals were carried out using shucked clams as diet at three temperatures (averages: 8.2, 16.7. and 18.7 C).

In addition, whole annelids were fed at a temperature of 14.7 C and mackerel flesh at a temperature of 18.7 C. Although the analyses of the *Limanda* results had shown no significant temperature correction, we eliminated the lowest temperature group from our analysis of these *Kareius* data since our metabolic studies had shown extremely high variability among these data, partly attributable to inclusion of the lowest temperature group. Even so, in the remaining 25 fish, individual variability was so high that it was not possible to detect any significant relations between metabolism and body size. With the small range, averaging for size groups as in the earlier analyses made no appreciable difference.

Under these conditions it is hardly surprising that in the statistical analysis described here we failed to detect strong relations among the log K and other variables. However, the analysis, over all diets, indicated a negative slope of log K with R and W greater than would have been expected fortuitously, although neither R nor W alone could be used to predict it. The relationship was also significant within the clam diet alone, but not within the annelid or mackerel flesh diets.

The data for individuals are plotted in Fig. 2 where the reasons for low correlation coefficients are apparent. The average values for various diets calculated in various forms are, however, of some interest in themselves. Thus, a comparison of the top panel where the calculations are made in terms of caloric equivalents, with the middle panel where the calculations are in the form of grams of wet weight and rations, suggests that in comparing different food materials containing different amounts of calories per grams, failure to correct for calorie equivalents may indeed give a misleading estimate of the relative values of different foods for growth. In this case the mackerel flesh calculated in wet weight appeared to be utilized with higher-than-average efficiency. However, expression in caloric equivalents suggests that the efficiency of its utilization for growth may not be significantly different from the efficiency of utilization of other foods when we take into consideration total intakes in equivalent energy terms. It is unfortunate that the data do not permit a more exact specification of relations among the variables, but it is of possible significance that the average growth efficiency for *Kareius* fed on the low calorie per gram clam diet (Fig. 2a) seems to have been of the order of 1.5 times that of *Limanda* fed on the higher calorie per gram annelids diet (Fig. 1a), at a common rations intake of about 100 kcal/20-day period.

Menzel's Reef-Fish Experiments

Menzel's (1960) experiments with a Bermuda reef-fish were carried out on groups of 6–12 individuals. Experiments were performed with three size groups at two different temperatures and two size groups at a third temperature. The experimental fish were fed on three different species of small fish, presumably whole dead ones; it is not clear from the description of the experiments how different food types were distributed in the temperature series, but they may have been partially confounded with temperature. The rate of

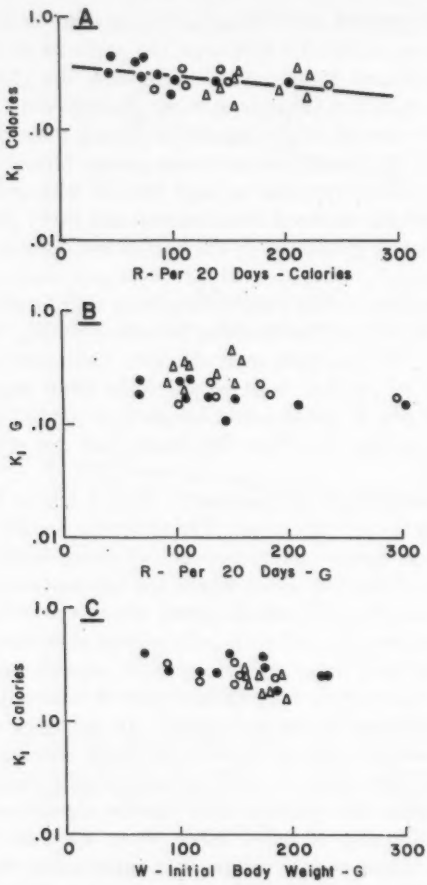

FIG. 2. Relation between growth efficiency, rations, and body weight in the Japanese plaice, *Kareius bicoloratus*. Plotted points are the data for individuals (see Fig. 1 for definition of terms): ● — shucked clams; ○ — annelids; △ — fish flesh.

feeding used was one in which the groups of fish were permitted to feed *ad libitum* for 1 hr a day, after which remaining food was removed from the tanks. Caloric equivalents of food consumption and growths of the groups of fish are given.

Analysis of covariance for the various size groups of fish within temperatures showed a significant effect of temperatures on the mean level of log K. Otherwise, the results are similar to those from the grouping of Hatanaka's *Limanda* data. That is, within temperatures there was a significant simple

negative correlation between log K in terms of calories and both R (weight) and W. However, the range of W was again greater, its correlation with log K higher, and with a positive correlation of about 0.90 between R and W, the partial regression again associated the decrease in log K with the increase in W. If the simple correlation between log K and R reflects a real, direct relationship, it is apparent that these experiments too would have to be carried out using a greater range of feeding levels in order to establish it. At the one feeding level body weight was the more efficient predictor of growth efficiency. Results plotted in Fig. 3 show that the relationships are again well described by straight lines.

Gerking's BlueGill sunfish Experiments

Gerking (1952) describes results of a 50-day feeding period with nine individual sunfish of two species. Except at the beginning of the experiment they were fed *ad libitum*. Food used was the meal worm, *Tenebrio*. Temperatures varied less than ± 1.5 C degrees from an average of 25 C. Two of the fish were observed in the summer of 1950, the rest in 1951. The food consumption and weight changes are given in terms of nitrogen contents. Analysis of these data indicates that 90% of the total variation in gross growth efficiency in

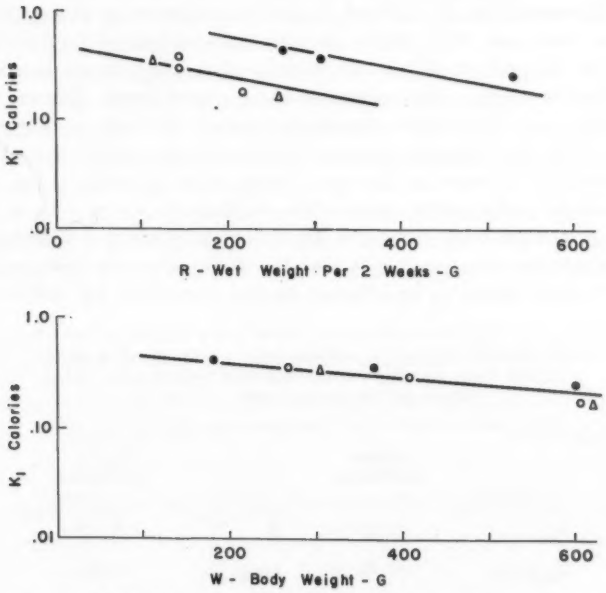

Fig. 3. Relationship between growth efficiency of groups of a Bermuda reef-fish and their rations and body weights, at various temperatures (data from Menzel 1960): ○ — 19 C; △ — 23 C; ● — 28 C.

terms of nitrogen retained was accounted for by the overall regression on nitrogen consumed and initial body weight. There was no significant difference between the species. The simple negative correlation of log K with R and W was, at this one feeding level, again assignable to the relatively much larger body weight change on the basis of the partial correlation coefficients. Gerking observed the relation to body weight and interpreted it as reflecting increasing "physiological age."

A similar, more extensive set of experiments was reported in a second paper (Gerking, 1955) using 20 bluegill sunfish, fed individually at five different rates from near maintenance to *ab libitum* feeding for periods of about 30 days. Two sets of experiments were reported, one conducted in the autumn with 10 fish at a temperature of about 23 C. The remaining 10 fish were observed in summer at about 26 C. Gerking again analysed his results in terms of nitrogen consumption and retentions and concluded that efficiency of retention (growth) increased with amount consumed. He also noted changes in water content and fats, and in his tables, in addition to the nitrogen data, he gives data on food and growth in terms of total dry weights, although he does not deal with them directly in these terms.

We have reanalyzed his data in terms of the dry weights of rations and growth. From the results it appeared for the autumn experiments that for feeding rates above the maintenance level there was no significant change in log K. However, log K showed a significant decrease during the summer experiments, and over 50% of the decrease was accounted for by the multiple regression on W and R. With the variety of feeding levels introduced into the experimental design, the results of these experiments differed from those described above, in that there was no significant correlation between W (dry weight) and R (dry weight) ($\mathbf{r}_{R,W} = +.21$). Furthermore, the experimental range of values of R was in this case higher than was the range of W. The resulting simple and partial correlation coefficients are given in Table IV, where it is seen that with the eight observations there is a significant simple negative correlation between log K and R (–0.67), but not between log K and W (–.40). Neither seems to be affected by the correction for differences in the

TABLE IV. Correlation coefficients, **r** and **R**, for bluegill sunfish from Gerking's (1955) summer experiments. Other symbols are the same as used in Table III.

	Simple correlation		Partial correlation
$\mathbf{r}_{\log K,R}$	–0.67*	**R**	0.72*
$\mathbf{r}_{\log K,W}$	–0.40	$\mathbf{r}_{\log K,R/W}$	–0.65
$\mathbf{r}_{R,W}$	+0.21	$\mathbf{r}_{\log K,W/R}$	–0.36

*Significant at the 5% probability level.

other variable as shown by the partial correlations. However, with only eight observations the values of the partial ($r_{\log K,R/W} = -.65$) could have arisen by chance in between 5 and 10% of cases. The data thus suggest that if the design of the experiment is such as to remove confounding of the level of rations intake with body weight, rations level alone may determine growth efficiency, independent of body weight changes. Unfortunately, these few observations are by themselves an insufficient basis for assessing the relative importance of the factors.

Kinne's Desert Pupfish Experiments

The feeding and growth experiments described by Kinne (1960, 1962) were carried out using groups of 6–12 fish per tank, held for periods of up to 22 weeks each in a series of five constant temperatures (15, 20, 25, 30, 35 C) at a salinity of 35‰. Salinities of 0 and 15‰ were also tested at 30 C, and 0‰ at 20 C. Observations of growth in length and food intakes were made at 2-week intervals and converted into terms of dry weight equivalents. Conversions of length of fish to equivalent weight measurements were made from tables kindly supplied by Dr Kinne. The results therefore offer information on growth efficiencies which are partially freed from effects of individual variability from time to time, and cover a more extensive range of constant conditions than any of the other experiments examined above. The groups were fed to satiation on *Euchytraeus* once a day (except Saturday and Sunday), then about 50% more food was added to the tank.

In the reanalysis of these data we have initially eliminated the data for the 15 and 35 C groups since our metabolic studies suggested that in these extreme conditions the fish reacted differently than at other temperatures. The resulting correlation coefficients for the remaining three temperature groups at 35‰ salinity are set out in Table V.

In the overall temperature series the first column shows that in keeping with the experiments reviewed above there was a high simple negative correlation between log K and both R and W. So also was there a high, positive

Table V. Correlation coefficients **r** and **R** in the desert pupfish held at a salinity of 35‰ at 20, 25, and 30 C. There were 47 observations on groups of 6–12 fish each (Kinne, 1960, 1962). Symbols are defined in Table III.

	Simple correlations			Partial correlations	
	Overall temperatures	Within temperatures		Overall temperatures	Within temperatures
$r_{\log K,R}$	−0.93**	−0.81**	**R**	0.93**	0.81**
$r_{\log K,W}$	−0.77**	−0.71**	$r_{\log K,R/W}$	−0.81**	−0.57**
$r_{R,W}$	+0.87**	+0.88**	$r_{\log K,W/R}$	+0.17	+0.02

simple correlation between R and W. In this case, however, the feeding conditions induced a relatively large percentage change in the rations, R, and in the third column the partial correlation between log K and R when W was held constant reduced the apparent effects of R by little (from −0.93 to −0.81). On the other hand, when R was held constant, the relation between log K and W became a nonsignificant positive correlation.

The effect of temperature was tested by covariance analysis, the results showing a significant effect of the temperature of the mean log K. When this was removed, the fourth column showed that there was a general weakening of the correlations due to the complete confounding in the experiment of the temperature with mean W, resulting in a much reduced range of W and R within the temperature groups. Despite this, the negative partial correlation between the log K and the R is still highly significant within temperatures, while the partial correlation between log K and W remains nonsignificant. When, as shown in the second column, we deleted the apparently superfluous body weight variable, the simple correlation between log K and R within the temperature groups was raised to −0.81 compared with the partial correlation of −0.57. The remaining simple correlations within temperature groups are included for comparison.

From these results it again appears that either the ration or the body size is sufficient for predicting growth efficiency. However, the analysis shows first, that despite the fact that only one feeding regime was used, the temperature changes induced a major change in the amount of food consumed. This situation persisted long enough that at the highest temperatures the fish apparently completed a major part of the growth characterizing the species. With this situation we have found that a knowledge of the rations intake specified growth efficiency more accurately than a knowledge of body weight. In fact, the body weight information did not appear to add substantially to prediction of growth efficiency if rations were known. Second, the similarity of results overall and within temperatures suggests that although different-sized fish apparently had different rations intakes in the different temperatures, the physiological compensations accompanying it were such as to permit prediction of the growth from rations using a single linear relationship.

These effects are more clearly assessed from our plots of Kinne's data in Fig. 4. In this figure we also show data for the 15 and 35 C temperature groups omitted from the calculations. As was observed in the metabolic study, the results for these groups clearly fall outside the trends established in the 20 to 30 C range. Within this range the data are adequately described by the single straight line. From the range of values covered by the different temperature series it appears that the significant covariance adjustment for temperature on mean log K resulted from the fact that the temperature differences induced different ranges of rations intake with corresponding differences in mean efficiency. The change did not affect the slope or position of the overall relationship between growth efficiency and rations.

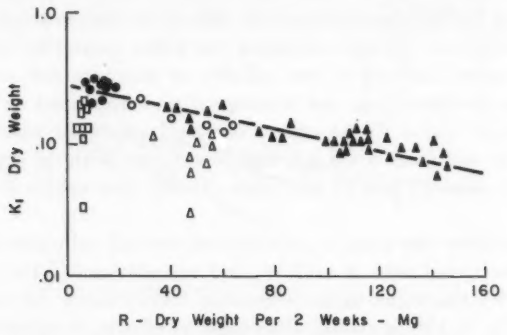

FIG. 4. Relationship between growth efficiency and rations in groups of the desert pupfish at different temperatures (Kinne 1960, 1962): □ — 15 C; ● — 20 C; ○ — 25 C; ▲ — 30 C; △ — 35 C.

This suggestion is confirmed by reference to the regression analysis. The overall partial slope of log K on R, eliminating W was $-.0050 \pm .0010$, whereas the partial slope within temperature groups was $-.0037 \pm .0016$. While the latter is slightly less well established than the former, there is no evidence of a difference in the relationship within temperature groups from the general overall relationship. We may conclude that under the specified feeding regime temperature was primarily important through its effect on amount of rations consumed.

It remains to determine whether inclusion of the body weight variable significantly alters the slope of the relationship between efficiency and rations. To study this we may compare the above partial slopes holding W constant, with the corresponding simple slope between log K and R. These simple slopes with their standard deviation are $-.0044 \pm .0005$ over all temperatures, and $-.0036 \pm .0007$ within temperature groups. As was the case with the partials, these values for the simple slopes are not significantly different from each other, indicating again that temperature affected efficiency through its effect on total food consumed. Neither are these simple slopes different from the comparable partial slopes. Eliminating the superfluous body weight variable has, in fact, markedly improved the accuracy of estimate of the relationship between log K and R.

It seems safe to conclude that in this series the log efficiency of growth was dependent in simple linear fashion on the amount actually consumed by the fish. Body weight appeared as a significant variable primarily because within activity levels due to temperature it was highly correlated with amount consumed. Evidently body weight can be used to predict growth efficiency where observations on rates of feeding at a particular size have been restricted, because at one such level the rations and weight are highly correlated. However, where food supply itself is changed and this correlation becomes weak, recourse must be had to the underlying efficiency–rations relationship.

In addition to his observations on effects of temperature, Kinne reports size, growth, food, and growth efficiency for fishes reared in various salinities. Some of these were hatched in one salinity or temperature and reared in another. From our examination, the rearing salinity appeared to be of overriding importance and in Table VI we report our analysis of the observations on fish reared at 30 C in salinities of 35, 15, and 0‰, taken without regard to hatching salinities from tables 13 and 15 of Kinne (1960), and tables 4 and 5 of Kinne (1962).

It appears from the simple correlations overall salinities that log K was only weakly associated with R and W, and calculations of the partials reduces these to levels which might frequently arise fortuitously. As can be seen from inspection of Fig. 5, this is partly the result of effects of salinity. After covariance adjustments for effects of salinity on mean log K, the correlation coefficients within salinities, given in the second and fourth columns, suggest that the effects of R were of major importance.

TABLE VI. Correlation coefficients **r** and **R**, in the desert pupfish at 30 C reared in salinities of 0, 15, and 35‰. There were 58 observations on groups of 6–12 fish each (Kinne, 1960, 1962). See Table III for definition of other symbols.

	Simple correlation			Partial correlation	
	Overall salinities	Within salinities		Overall salinities	Within salinities
$r_{\log K,R}$	−0.37**	−0.69**	**R**	0.37**	0.71**
$r_{\log K,W}$	−0.35*	−0.50**	$r_{\log K,R/W}$	−0.14	−0.57**
$r_{R,W}$	+0.89**	+0.86**	$r_{\log K,W/R}$	−00.5	+0.22

The effects of salinity appear greater and of a rather different type than those due to temperature. The data plotted in Fig. 5 suggest that the low correlations in the overall data result from the fact that a change in salinity level was accompanied by a highly significant change in mean level of log K, irrespective of the level of R. When this salinity effect was removed the simple negative correlations of log K on R and W were clearly discernible, although the partial correlations again suggest that the negative correlation with W is the result of the correlation between W and R. However, the relations are generally weaker than in the study in 35‰ alone and from the plot of observational data in Fig. 5 it appears that there may have been a difference in the slope of the log K, R line with change in salinity. This effect is more clearly assessed from Table VII where we set out the pertinent data for each of the sets of salinity observations separately.

These results clearly indicate that the negative correlation between log K and R ($r_{\log K,R}$) does not depend on W ($r_{\log K,R/W}$). However, the

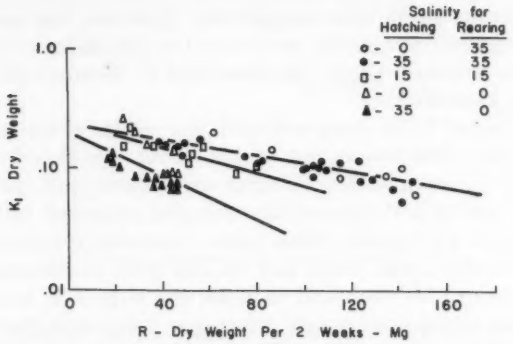

FIG. 5. The relation between growth-efficiency and rations in the desert pupfish under different salinity conditions at 30 C (data from Kinne 1960, 1962).

TABLE VII. Correlation, r, and regression, b, coefficients under various salinities in desert pupfish reared at 30 C.

Salinity (‰)	No observations	$r_{\log K,R}$	$r_{\log K,R/W}$	$r_{\log K,W}$	$r_{\log K,W/R}$	$b_{\log K,R}$	$b_{\log K,R/W \pm 2\sigma_b}$
35	29	−0.87**	−0.70**	−0.75**	+0.03	−.0034	−.0035 ± .0015
15	8	−0.81**	−0.68**	−0.74**	+0.55	−.0053	−.0178 ± .0070
0	21	−0.56*	−0.75**	−0.01	+0.61**	−.0095	−.0175 ± .0071

relationship with W ($r_{\log K,W}$) which appears significantly negative in the higher salinities shows a rather different relationship with log K when effects of R are removed ($r_{\log K,W/R}$). While the partial correlation of log K with W is not significant at the 5% probability level either in the salinity of sea water, or at 15‰, it is high at 15‰, and in fresh water is a significantly positive correlation at the 1% probability level. That is, irrespective of the effects of the level of feeding, in the lower salinities the larger fish showed a significantly greater growth efficiency. The last two columns of the table show that the apparently altered simple slope observed in the plot of observations in Fig. 5 is verified by the partial slopes, the partial slopes for 15‰ and for fresh water being significantly higher negatives than that found in salt water.

We thus conclude from this further analysis of Kinne's observations that in the salinity of sea water growth efficiency depended simply upon the food consumption. Within the normal temperature range of the species this relationship was unaffected by temperature, except indirectly through the effects of temperature on the food consumption. In lowered salinities the average growth efficiency of the fish was reduced, but in addition the depressing

effects of rations on log K were exaggerated. However, the simple expression of this depressing effect was partly ameliorated by the influence of body weights. That is in lower salinities larger fish were able to maintain their growth efficiency better than small fish.

These results are to be compared with the results of our metabolic study of these same data (Paloheimo and Dickie, 1966). These indicated that at a salinity of 35‰ the relationship between metabolism and body weight, and its response to feeding and temperature changes, appeared to be the same as its characteristic of warmwater fishes under nonstress conditions. In lowered salinities on the other hand, there was an elevation of metabolic rate which was relatively greater for the small than for the large fish, leading to a slope of log metabolism on log body weight which was lower than that which seemed characteristic of warmwater fishes. The results, in combination with these investigations of growth efficiencies, suggest that the lowered salinities induced a relatively greater metabolic expenditure among the small fish, and that this took place at the expense of energy for growth.

Cortland Hatchery Brook Trout Experiments

Data on hatchery feeding of brook trout in large experimental troughs have been reported in a number of publications of the Cortland Hatchery. Biweekly results of the experimental feeding of several trial lots over a period of about 22 weeks are reported by Tunison et al. (1939), and Phillips et al. (1940). From information given in the former report it appears that over 1000 fingerlings were started in each experimental lot and fed approximately 8% of their initial weight each day. At 2-week intervals a sample of the fish was weighed and enough of them then removed from the tank to bring the total contained weight of fish back to the original starting weight. The feeding rate per unit weight of fish was held constant, as was the temperature (13 C). Our metabolic examination of these data indicated no significant differences between the different diets in the different trial lots, nor between years. At the beginning of all the experiments the feeding level appeared to have induced a level of metabolism only slightly above a maintenance level. During the experimental period, however, this level rose progressively and at the end had reached what appeared to be maximum sustained metabolic level.

Since the feeding was proportional to body weight, there is, of course, no difference between the regression of log K on either R or W. However, the overall correlation coefficient between log K and R of –0.79, and the slope of the regression line in terms of biweekly rations of $-.0281 \pm .0034$, confirms that for the mass feeding of brook trout the relationship is adequately described by a simple straight line. The data are plotted in Fig. 6.

The analysis of the growth–efficiency changes indicated, as with the metabolic study, that there was no significant difference in the growth–efficiency–rations relations between the diets, nor from year to year. No data on caloric equivalents are given which would provide a basis for judging the importance of this observation. However, the form of administration as a

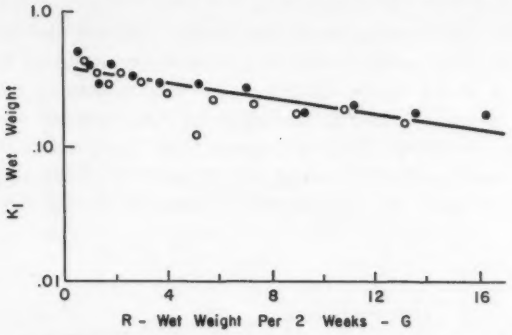

FIG. 6. Growth efficiency in relation to rations in the brook trout (data from Cortland Hatchery reports for 1939, 1940); ○ — 1939 experiment; ● — 1940 experiment.

mash, bound with a small addition of gelatin, was apparently the same in both years, and from the general description given the diets may have been very little different. From our point of view the most significant result is that the growth–efficiency regression on ration appears adequately described by a straight line, despite the fact that the metabolic studies indicated a progressive change in metabolic level.

OTHER EXPERIMENTS

We have plotted the logarithm of the gross growth efficiency against rations from several other published studies in which the data do not appear to warrant detailed statistical analyses. The results of a least some of them confirm those obtained from the foregoing more detailed study. For example, Karzinkin (1952) reports results of the hatchery rearing of several groups of young inconnu in which differences in level of feeding were apparently the result of differences in holding temperatures as in Kinne's experiments. The results plotted in Fig. 7 are again well described by a single straight line

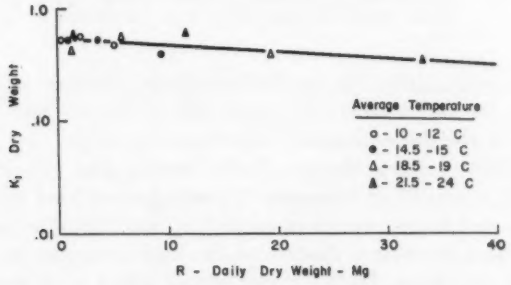

FIG. 7. Growth-efficiency, rations relationship in groups of young inconnu reared in hatchery tanks (data from Karzinkin, 1952).

and show a significantly negative slope. Similar data on the feeding of groups of young carp on chironomid larvae in a pond were published by Ivlev (1939). The data in Fig. 8 are again described by a significantly negative straight line, despite a normal seasonal variation in temperature conditions. From data reported by Winberg (1956) it appears from our plots that similar results were obtained from hatchery feeding and growth of young carp by Krivobok (Fig. 9) and of mature male *Leucaspius bilineatus* during the post-spawning

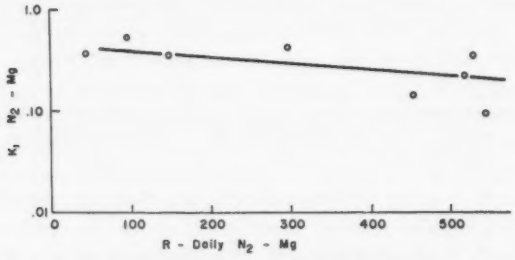

FIG. 8. Growth-efficiency, rations relationship in a group of 1-year-old carp fed in a pond on chironomid larvae (Ivlev, 1939).

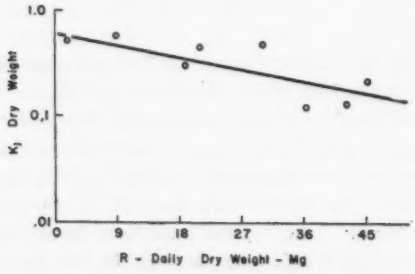

FIG. 9. Growth-efficiency, rations relationship in a group of hatchery- reared young carp (data from Winberg, 1956, after Krivobok).

period by Yablonskaia (Fig. 10). In the latter case, the data for females appear similar to those for males except for one value of low efficiency on low rations during the last of the three-biweekly observation periods.

Baldwin (1956) reports results of the feeding and growth of individual brook trout fed on small live minnows. Three fish were held for a month each, at each of three test temperatures in ascending and then descending sequence. A fourth fish which developed disease at the high temperature was thereafter eliminated from the series. Data for two others which were tested only at the lowest temperature were given in his tables. Our analysis of these results confirmed Baldwin's conclusion that there was a high correlation between rations

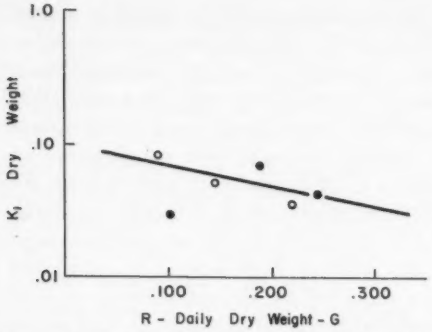

FIG. 10. Growth-efficiency, rations relationship in sexually mature *Leucaspius bilineatus*, during the post-spawning period (data from Winberg, 1956, after Yablonskaia): ○ — male; ● — female.

and body weight, and showed that temperature had a small but significant effect on mean growth efficiency. However, the simple regression between log efficiency and both rations and body weight was significant only at the highest temperature. The overall data plotted in Fig. 11 appear to be described by a simple straight line with no detectable slope.

A somewhat similar result was obtained from Surber's (1935) data on a group of brook trout and of rainbow trout held at a constant temperature of 12 C and fed on live *Gammarus*. Data on average body size, growth and food consumption are given at monthly intervals for a 5-month period. In both cases the data suggest a negative relationship between log-efficiency and both rations and body weight, but the five points for each are insufficient for a critical test of any such hypothesis. The data for the brook trout are plotted with Baldwin's data on Fig. 11.

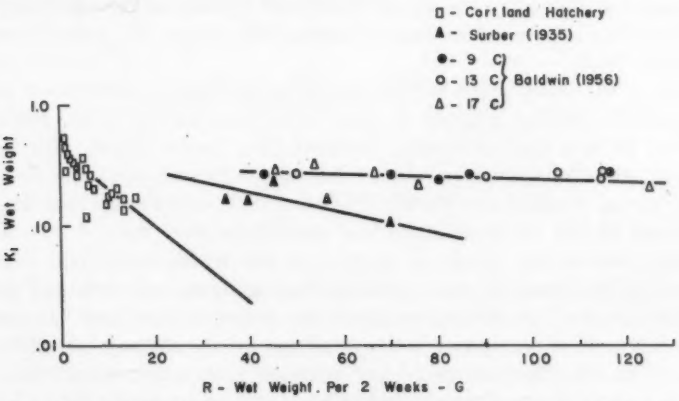

FIG. 11. Relationship between growth efficiency and rations in the brook trout fed on three different diets.

No significant relationships could be found in several other sets of published data. Karzinkin's (1952) data on consumption and utilization of nitrogen by 4-year-old roach, calculated from the analysis of small samples taken from Lake Glubokoe at biweekly intervals, give what Winberg (1956) termed a random scatter of values of growth efficiency. Similar data given by Karzinkin on the growth and feeding of young pike on *Daphnia* and minnows showed no relationship between growth efficiency and rations. From his examination of the apparent metabolic relationships Winberg concluded that in both cases there were errors in the calculated food consumptions, especially at the smaller sizes and feeding rates. Similar high scatter of calculated growth efficiencies characterize the data reported by Brown (1946b) on feeding of brown trout on both *ad libitum* and restricted rations at 13 C, and on cod at varying temperatures reported by Kohler (1964). In neither of these latter two cases did our metabolic study of the data reveal a significant relationship between metabolic rate and body size.

DISCUSSION

The foregoing review of data on growth efficiencies confirms the experience of other investigators that there are relatively large variations within individuals at different times, as well as differences between individuals. In the case of the Dawes plaice experiments, it is evident that a major part of such variations was associated with the seasonal temperature trends, effects of which were apparent not only in the growth efficiencies but also in the metabolic indices reviewed earlier (Paloheimo and Dickie, 1966). That is, there is little doubt that seasonal changes in environmental conditions affect the rates of turnover and the disposition of the components of the total energy system. Such effects may have resulted either from shifts in energy demands during acclimation to different conditions, or from differences in the energy distribution in the final (balanced?) states. In certain situations in nature, adjustments of this sort may be an important feature of the operation of the energy systems, hence, they deserve systematic study. At present we know little about them.

Even in the cases where environmental or holding conditions are constant and metabolic indices indicate a state of acclimation to them, the data of Pentelow, Brown, and Hatanaka indicate that both within- and between-individual variations are a persistent feature of growth efficiency data. Such variability was studied by Brown (1946a, 1957) who found that important components of the between-individual variations were related to the social hierarchies among her trout. In respect to the within-individual variability she demonstrated that there were regular fluctuations in growth and appetite, apparently related to deviations from an average condition factor. These fluctuations tended to restore body condition to its average value but with a time lag in the effectiveness of the regulatory response. Regulation of the growth of body parts or proportions has been implied for many years in allometric growth equations (Reeves and Huxley, 1945), but in keeping with Brown's

findings, Martin (1949) concluded that in fishes such regulation is modified by feeding conditions. Since rather clear-cut patterns in growth efficiencies emerge from average of results for several individuals or from data on groups of individuals, we conclude that much of the individual variability showing up in our analyses apparently reflects phenomena of the sort studied by Brown.

Feeding and growth data for groups and of numbers of individuals held under constant physical environmental conditions provide information on the nature of overall changes or trends in growth effiicency and the factors which may be responsible for them. Thus, in a number of experiments where several fish were exposed to a single food supply level and observed for a period of time, there appeared to be a steady decrease in the logarithm of the gross growth efficiency, i.e. log K. The data also show a high correlation between the progressively increasing rations, R, and body weight, W. However, during growth of a particular group of fish, there was a consistently greater range of values of W than of R. In such cases the result, revealed by our multiple regression analyses, was that body weight, W, was the more efficient predictor of growth efficiency. By contrast, in experiments where a variety of constant environmental conditions or feeding levels were tested over a comparable range of body weights so that the correlation between R and W was low, multiple regression analyses indicate that the level of rations, R, is the better predictor of log K, while the relationship with body weight seems to be of little or no significance. Such results offer strong support to the conclusion of Brown (1957) that food supply is the most important determinant of growth efficiency, and of Kleiber (1947, 1961) that body size is not a directly determining factor. The data available to us suggest, furthermore, that the relationship between log K and R is adequately described by the linear equation:

$$\log K = \log\left(\frac{\Delta W}{R\Delta t}\right) = -a - bR$$

or

$$K = \frac{\Delta W}{R\Delta t} = e^{-a-bR} \tag{3}$$

or

$$\frac{\Delta W}{\Delta t} = Re^{-a-bR}$$

This equation expresses growth as a function of rations independent of body weight. General considerations indicate that there must be practical limits to its applicability. For instance, a ration intake which is maximal for a small fish would mean starvation for a large one. The results reviewed here and by Paloheimo and Dickie (1966) suggest that the limits of applicability of this equation at given body weight may be determined by com-

parison of the growth efficiency or K-lines (equation 3) with the metabolic or T-lines (equation 2) derived from the same experimental data.

It was pointed out by Paloheimo and Dickie (1966) that with a given feeding regime under constant physical environmental conditions, fish of different sizes appear to adjust their food intakes and rations in such a manner as to maintain a constant metabolic level — α of the T-line. Changes in the feeding system, the temperature, or both, resulted in changes in α but did not appear to affect the exponent, γ, significantly. In the Kinne experiments in particular, comparison of the data on metabolic levels and growth efficiencies at different temperatures at a salinity of 35‰ shows that the increased temperatures resulted in increased rations which were in turn reflected in different values of α in the T-lines. However, despite these metabolic level changes, the different ranges of rations at different temperatures appear from this review to be described by a single K-line (Fig. 4). Similarly, single K-lines appeared to describe the relation between the growth efficiency and rations resulting from the experiments under different temperature of feeding regimes by Hatanaka et al. (1956a), Gerking (1955), Karzinkin (1952), and Baldwin (1956). Growth efficiency data from the Cortland Hatchery brook trout feeding were also described by a single K-line despite the fact that the system of feeding in proportion to body weight seems to have induced a rise in metabolic level from near maintenance to the active level (Paloheimo and Dickie, 1966). We conclude from such evidence that a K-line with given values of the parameters "a" and "b" describes the relationship between growth efficiency and different amounts of a particular type of rations from a level near maintenance up to and including the active metabolic level.

From such considerations it appears that recourse to experiments which have been designed to reveal the types of adjustment that fishes of different sizes make to various laboratory regimes provides us with a system of general relations which describe energy dispositions underlying the production system. That is, in a particular environmental situation we may describe the metabolic expenditure by the T-line:

$$T = \alpha W^{\gamma} \tag{2}$$

But in the balanced energy equation

$$R = T + \Delta W/\Delta t \tag{1}$$

We now find that

$$\Delta W/\Delta t = Re^{-a-bR} \tag{3}$$

By substitution we then have that

$$T = \alpha W^{\gamma} = R(1-e^{-a-bR}) \tag{4}$$

That is, we have a system of equations relating the metabolism, body weight, growth, and food consumed, in which the parameters are experimentally

determinable variables reflecting various physiological and behavioural characteristics of particular life-history stages of species in given environmental situations. It was on this basis that we used the system of equations (3) and (4) to outline the growth of fishes under constant conditions (Paloheimo and Dickie, 1965). The treatment is readily extended to other situations when information is available on the factors affecting α, a, and b. This was implied in our earlier treatment of growth by scaling the growth curves in terms of α and b in order to examine their general form.

The use of the K-lines and T-lines in this fashion implies that there are definable periods during which the parameters show reasonable constancy, or at least predicable variation. That is, we are implying that the processes of acquiring and using food energy follow rather regular patterns dependent on the rate of acquisition of that food energy. The formulation offers little information on the mechanism underlying this regularity, but suggests that it may be possible to study them in relation to the parameters α and γ of the T-line and a and b of the K-line. While it is obvious that this subject is one which requires further specific study, some appreciation of the factors which may determine the parameter values of the K-line can be obtained by comparison of results of the various experiments reviewed above.

It appears, first of all, that the relations between growth efficiency and rations intake reflect regulation of the total energy system in the animal rather than only a part of it. This is suggested especially by the contrast between the results of Gerking's (1955) measurements of the efficiency of use of nitrogen in relation to the nitrogen budget and our evaluation of total dry weight food consumption and usage in his experiments. Winberg noted an inexplicable variability in other attempts to use nitrogen balance techniques. There must be limitations to the flexibility of the metabolic system, but such evidence suggests that given a minimum variety and supply of nutrient materials the important limitation on production processes is the ability of the animal to marshal energy at various metabolic sites, and that this ability may be at least partly independent of the form in which that energy is stored and used.

The relationship of growth efficiency to intake does not appear to be a simple function of the bulk of the intake. This was implied in our review of metabolic relations (Paloheimo and Dickie, 1966) where it was suggested that intake was not a simple function of the degree of stomach filling or digestibility of the food. In the growth efficiency observations reviewed here, we note from Fig. 2A that for *Karius bicoloratus* there was no appreciable difference in the growth efficiencies per calorie intake for three foods: shucked clams, annelids, and chopped mackerel flesh having kcal/g contents as different as 0.68, 0.82, and 1.43, respectively. Furthermore, a comparison of Fig. 2A with 1A for *Limanda yokahamae* indicates that at a food intake level of 100 kcal/20 days on the same food type, the growth efficiency of *Kareius* was nearly twice that of *Limanda*, and the slope b of the K-line appears to have been rather larger for *Limanda*. We can only conclude that the growth

efficiency lines must reflect integration of possibly complex physiological and behavioural processes which act in the regulation of the energy system, and which may result in characteristic differences between species in the same environment.

It is also clear from the experimental results that the K–lines reflect the influence of certain features of the environment in different ways. It has already been noted that changes in temperature, while changing the metabolic level have in most cases not resulted in a change in either the slope or position of the K-line. That is, while changes in both temperature and food supply apparently give rise to a change in the total rate of turnover in the energy system, they do not in themselves give rise to a basic difference in the distribution of the energy among various metabolic components. In these cases the distribution and use of the input energy depends simply on the rate of supply. A possible exception is provided by the results of Menzel (Fig. 3) where the highest temperature resulted in a marked displacement of the K-line (i.e. "a" was greater) although, as was pointed out, this may also have involved experimental confounding with the type of food.

By contrast, the experiments reported by Kinne indicate that the effects of changes in salinity on the growth efficiency are quite different from those of temperature and food supply. In his experiments a decrease of salinity from 35 to 15‰ and to fresh water, appears to have resulted in a decrease in the general growth efficiency level, and apparently in the slope as well. This is in keeping with observations on the general physiology of fishes which show that such environmental factors may control the basic energy demand for maintaining osmotic and ionic balances. Similar effects are suggested by the work of Kawamoto et al. (1957) who reared fish in ponds at two different densities, one double the other. Rate of feeding per unit weight was the same in both tanks and while rate of growth had the same general pattern, it was appreciably lower at the higher density. While actual growth efficiency data are not given, it was apparently lower at the higher density. The experimenters attributed the difference to a greater metabolic load, related to a higher concentration of nitrogenous wastes in the tanks with the higher density of fish.

A comparison of the results of the feeding of brook trout on different foods suggests that one of the most important factors affecting the parameters of the K-lines may be the type of food consumed, although in the absence of specific experiments we cannot surely differentiate the effects of this factor from those of other variables. Thus, the data assembled in Fig. 11 show that feeding of young trout on a hatchery mash resulted in a K-line with a relatively steep slope. A simple extrapolation of this line indicates that if the experiments had been continued longer, the growth efficiency would have been reduced to about 1% by the time food consumption reached 50 g/2-week period. This would hardly have sustained growth rates comparable with those found in nature without large increases in food consumption. However, our earlier metabolic studies of the Cortland Hatchery data showed that the fish were, at the end of the experiments, already operating at the maximum metabolic

level, so that food consumption on this type of food could not have increased much unless their ability to pick up food per unit metabolic expenditure became greater. Surber's results show, however, that when trout were fed on *Gammarus*, the average growth efficiency increased to about 16% and possibly that the slope of the K-line was much reduced. Baldwin's feeding with minnows resulted in a further increase in growth efficiency to about 25% with a further decrease in slope. In both these latter cases, the metabolic studies indicated that the metabolic level was at its maximum, hence the higher growth efficiency on the new foods was not resulting from a higher total metabolic output relative to their size. Rather, for a particular amount of food intake, the shift in food type led to a large increase in the proportion of the food energy available for growth without changing the total metabolic expenditure.

Such marked changes in the K-line with change in food type without effect on overall metabolic level suggests that the underlying mechanism involves the efficiency of the grazing, i.e. the caloric reward for a particular behaviour pattern, rather than a simple physiological or digestive efficiency change. It is, therefore, of considerable interest to interpretation to note the results of experiments of Ivlev (1961). He found that when he increased the variance of the distribution of food particles in a tank the fish were able to obtain more food per unit time, the increase in variance having as great an effect on grazing success as did increased average food density in the tanks. While he did not measure metabolic rates in the various experiments, he had earlier (Ivlev, 1944) demonstrated that the rate of swimming in tanks is apparently independent of the food density over a wide range of densities. It is tempting then to speculate that in the trout experiments the shift in feeding from hatchery mash to *Gammarus* to minnows was equivalent to an increase in the variance of the distribution of food particles. That is, the increase in growth-efficiency was importantly related to the fact that the fish were obtaining food in larger particle sizes or chunks, hence a higher calorie intake per expenditure of energy for grazing.

While such explanations for the importance of food type are still only speculation, the need for studying them in relation to production in natural communities is underlined by the findings that species change their diets in more or less predictable fashion during their lifetime (Chrzan, 1962; Powles, 1958). The pattern of change may show the influence of seasonal and year-to-year differences in the food arrays (Ivlev, 1961) or in the amounts available per grazer (Nikolskii, 1962; Strzyewska, 1962). However, there is little doubt that they are importantly linked with growth phases or stanzas (LeCren, 1958; Parker and Larkin, 1959). The importance of these changes might well be reflected and measured in terms of their effects on parameters of the K-line.

The discussion of the significance of food types on K-lines cannot be left without noting again that if, in nature, the food supplies for young fish resulted in slopes as high as those characterizing the Cortland Hatchery mash, sustained growth would be impossible. Diet changes which would result in much lower slopes would appear to be an essential condition. These lower

slopes would be difficult to measure experimentally, and in keeping with this we could not be certain from the Surber and Baldwin data whether there was a significant slope. Nevertheless, the fact that decreasing growth increments are frequently encountered among large fish at advanced age and size, while there is no evidence of starvation or of decrease in metabolic levels, makes it seem likely that decreases in growth efficiency rather than food limitations are the responsible factors. That is, it seems that both "a" and "b" of the K-lines are likely to be important parameters throughout the life history of fishes.

It is unfortunate for our discussions that the data available do not give us the opportunity to differentiate clearly between effects of food types and density of the feeding populations. Menzel's and Kinne's experiments were carried out using different group sizes without apparent influence on the efficiencies. However, the large differences between the trout studies may have partly resulted from the fact that the Cortland tanks held several hundred fish each, Surber used four fish per tank, and Baldwin observed isolated fish. In addition to the well-known effects of crowding on growth and metabolic levels, Brown observed that the success of individuals depended on their position in social hierarchies and Kodama (1960) concluded that social organization may in some cases make feeding success of individuals less dependent on food distributions.

CONCLUSIONS

In conformity with the apparent conservatism of relations among metabolic components of the basic energy system (Paloheimo and Dickie, 1966), we have found that for a number of species within a given type of food the logarithm of the fraction of total energy intake used for growth is inversely linearly related to the amount of food energy consumed. This we express in the form

$$\log K = \log \Delta W/R\Delta t = -a - bR$$

or

$$\Delta W/\Delta t = Re^{-a-bR} \tag{3}$$

which we have termed the K-line. If this simple relationship should be confirmed, it appears that we have yet another sensitive manifestation of the integrative-regulatory mechanisms by which fish maintain themselves. However, in contrast with the stable slope of the metabolism–body weight relation, it appears in the case of the growth efficiency curves that within the basic linear pattern there is considerable potential for differences. The experimental data available demonstrate that such differences may show up either between species feeding on the same food or between types of foods for the same species. This suggests that observed parameter values for particular situations may provide important characterizations for the animal's position in the natural production chain. That is, while most fishes appear to operate within a common metabolic framework, the factors which lead to particular parameter values

for the K-lines may reflect the different abilities of species in natural communities to obtain and to use food energy for their maintenance and production.

From this point of view, better knowledge of the mechanisms underlying the parameter changes appears to be essential to an understanding of the processes of natural production which man wishes to use to his own advantage. Elucidating the mechanisms underlying the relations is obviously not a simple matter, and requires more information than we now have. However, some interpretations of possible value in designing future investigations can be made on the basis of data available.

We conclude first of all that the linear decrease in growth efficiency with increasing rations is not a simple result of changes in digestive efficiency of a given degree of stomach filling. At a fixed body size and ration, growth efficiency values based on bulk measurements may differ widely with the type of food consumed, although these differences may disappear if the calculation is carried out in caloric equivalents. By contrast, growth efficiency levels between species do not necessarily seem to be related to the caloric content of the food. These observations, in conjunction with the conclusions from our metabolism study that the control of food intake for metabolism was dependent on the total energy level rather than the degree of stomach filling, suggest that the efficiency curves are reflecting the influence of the metabolic cost of particular behaviour patterns on the distribution of the energy intake within and between fishes of a feeding group.

Particular environmental factors appear to have different effects on the efficiency and metabolic curves. Temperature and food affect metabolic level, but within the normal metabolic range do not appear to alter the parameters of the growth efficiency curves. This suggests that they affect the general rate of turnover of energy perhaps by a general effect on physiological and behavioural activity, but do not change its pattern of distribution. On the other hand, salinity and nitrogenous waste products appear to alter the position and slope of both metabolic and growth efficiency curves, an indication of their role in changing the basic distribution of energies. Changes in population densities or social hierarchies may have similar double roles, although the data available do not provide us with information on their effects.

Of all factors influencing the parameters of growth–efficiency curves, types of food appear to have the greatest potential effect. We interpret this as a reflection of the direct interaction between the energy expenditure necessary in the activity of procuring and converting food into fish flesh, within a fixed total metabolic level, and the rewards of this activity. It remains, however, to be demonstrated whether the differences in energy requirements of different behaviour patterns, and the energy rewards of different food particles sizes are sufficient to account for the experimentally demonstrated sharp differences in the growth efficiency curves.

We conclude in general, that in any life-history phase and environmental situation in which fish characteristically select certain types of food, the physiological and behavioural processes underlying growth may find rather

simple and stable expressions in growth efficiency curves (K-lines; equation(3)). If this is confirmed, we may infer that the position of this life-history phase in the production complex of the natural community can be specified and studied. Combined with a knowledge of metabolic relations in the balanced energy equation, it provides a system of relations which permit specification of the production of fish flesh by growth, in relation to the supply of food energy. It is on this basis that earlier (Paloheimo and Dickie, 1965) we outlined a simple, albeit possibly oversimplified, formulation of growth in fishes.

ACKNOWLEDGMENTS

We wish to express our thanks to Dr J. L. Hart, Director of the Biological Station, St. Andrews, N. B., whose interest and active support made it possible to continue this work. This paper, as well as the two earlier papers of the same series, were prepared at the University of Toronto in facilities provided by the Department of Zoology. We gratefully achnowledge the kindnesses of Dr K. C. Fisher, Chairman of the Department of Zoology, and Dr G. B. Langford, Chairman of the Great Lakes Institute, who made this arrangement possible. It is a special pleasure to acknowledge our indebtedness to Dr F. E. J. Fry, Department of Zoology, for helpful suggestions during the preparation of this and earlier manuscripts.

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Steroid Transformations by Corpuscles of Stannius of the Atlantic Cod (*Gadus morhua* L.)[1]

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ABSTRACT

Corpuscles of Stannius tissue of Atlantic cod (*Gadus morhua* L.) transformed [4–^{14}C] pregnenolone to progesterone and [4–^{14}C] progesterone to 11-desoxycorticosterone *in vitro*. These results establish the presence of 3β-hydroxysteroid dehydrogenase, Δ^5-3-ketoisomerase and 21-hydroxylase. Transformation of the ^{14}C-steroid precursors to several as yet unidentified substances also occurred.

INTRODUCTION

For many years there has been a controversy concerning possible adrenal-cortical function for the corpuscles of Stannius of fish. They are sometimes called the "posterior interrenals" because of their morphological position on the surface of the kidney and because they show histological characteristics normally associated with endocrine function (Rasquin, 1956). There is a phylogenetic progression from 40 or 50 corpuscles in the Holostei to a single pair in the more specialized teleosts (Garrett, 1942). Cod were generally found to have a single pair of corpuscles. It has also been reported that corpuscles of Stannius are concerned with osmoregulation in fish (Rasquin, 1956) and participate in the regulation of water–mineral balance (Olivereau, 1963).

Several unsuccessful attempts have been made to isolate (Ford, 1959; Chester Jones and Henderson, 1965), and to effect the *in vitro* synthesis of, adrenocorticosteroids from corpuscles of Stannius (Phillips and Mulrow, 1959; Sandor et al., 1966). Other investigators (Botte et al., 1964; Chieffi and Botte, 1963; A. S. Grimm, unpublished data[2]) have failed to demonstrate histochemically the presence of 3β-hydroxysteroid dehydrogenase, an enzyme necessary for steroidogenesis. In spite of the unsuccessful search by some investigators, others (Fontaine and Leloup-Hatey, 1959; Cédard and Fontaine, 1963) claim to have demonstrated the occurrence of steroids in this tissue.

The purpose of the present investigation was to determine if any of the enzyme systems necessary for synthesis of recognized biologically active steroids are present in the corpuscles of Stannius of the Atlantic cod (*Gadus morhua* L.). In agreement with Chester Jones et al. (1965), it was thought

[1]Received for publication June 30, 1966.

[2]Dr A. S. Grimm, a postdoctoral fellow at this laboratory, failed to demonstrate 3β-hydroxysteroid dehydrogenase histochemically in corpuscles of Stannius from the fish used in this study. Pregnenolone, pregnenolone sulfate, dehydroepiandrosterone, and dehydroepiandrosterone sulfate were employed as substrates and nitro blue tetrazolium, tetranitro blue tetrazolium, blue tetrazolium, and neotetrazolium chloride as hydrogen acceptors.

J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

desirable to continue the search for steroid biosynthesis in species not yet studied. The corpuscles of Stannius of the cod were chosen, in part because the principal hormone in cod blood is known (cortisol) (Idler and Freeman, 1965).

MATERIALS AND METHODS

Normal male and female cod 40–70 cm in length were killed by a blow on the head. The corpuscles of Stannius were excised quickly, chilled, and the extraneous tissue removed. They were quartered, weighed, and placed in oxygenated medium maintained near 0 C. Incubations were carried out under oxygen in a Dubnoff metabolic shaker for 3½ hr at a temperature of 20–25 C. Precursors used were either chromatographically homogenous [4-^{14}C] progesterone[3] (S. A. 146 μc/mg) or [4-^{14}C] pregnenolone (S. A. 145 μc/mg).

The incubation medium was that previously used successfully for fish interrenals (Idler and Truscott, 1966a). Two milliliters of medium were used for each 100 mg of tissue and 100, 143, and 456 mg were used with incubations 1, 2, and 3, respectively. One and one-half units of porcine ACTH, 1 mg of glucose-6-phosphate, 0.25 mg NADP, 0.25 mg $NADH_2$, and 1 mg of glucose-6-phosphate dehydrogenase were added per milliliter of incubation medium and cofactors were replenished after 1½ hr incubation. At the end of each incubation, 10 μg of 11-dehydrocorticosterone, corticosterone, cortisone, cortisol, 11-deoxycorticosterone, progesterone, 17α-hydroxyprogesterone, androstendione, 11β-hydroxyandrostendione, and testosterone were added. The incubation mixtures were diluted with water and extracted three times using 2.5 volumes of dichloromethane. The dichloromethane was flash-evaporated employing a water bath at 40 C and a dry ice–acetone chilled receiver. The residue, taken up in dichloromethane–methanol (5:1), was separated into fractions by thin-layer chromatography twice in one dimension on silica gel G (0.25 mm thickness) containing 0.5% Sylvania Electric Products Inc. No. 2282 green lamp phosphor. In the first solvent system, ethyl acetate: cyclohexane:toluene (10:10:1), the solvent front was allowed to run 17 cm from the origin and no wick was employed in the tank. In the second system, chloroform:methanol:water (90:10:1), the solvent front was allowed to run 15 cm from the origin and a wick was used. The areas which quenched fluorescense were removed using glass elutors (Matthews et al., 1962) and the steroids were recovered with methanol. A portion (ca. 1%) of each eluted area was

[3]Abbreviations and trivial names used: cortisol, 11β,17α,21-trihydroxypregn-4-ene-3,20-dione; corticosterone, 11β,21-dihydroxypregn-4-ene-3,20-dione; desoxycorticosterone, DOC, 21-hydroxypregn-4-ene-3,20-dione; progesterone, pregn-4-ene-3,20-dione; pregnenolone, 3β-hydroxypregn-5-ene-20-one; 11-dehydrocorticosterone, 21-hydroxypregn-4-ene-3,11,20-trione; cortisone, 17α,21-dihydroxypregnen-4-ene-3,11,20-trione; 17α-hydroxyprogesterone, 17α-hydroxypregn-4-ene-3,20-dione; androstenedione, androst-4-ene-3,17-dione; 11β-hydroxyandrostenedione, 11β-hydroxyandrost-4-ene-3,17-dione; testosterone, 17β-hydroxyandrost-4-ene-3-one; 20β-dihydroprogesterone, 20β-hydroxypregn-4-ene-3-one; 20β-dihydro-DOC, 20β,21-dihydroxypregn-4-ene-3-one; aldosterone, 11β,21-dihydroxypregn-4-ene-18-al-3,20-dione; 1α-hydroxycorticosterone, 1α,11β,21-trihydroxypregn-4-ene-3,20-dione; dehydroepiandrosterone, 3β-hydroxyandrost-5-ene-17-one.

counted for ^{14}C with an error of less than 5% in a Packard Tri-Carb Liquid Scintillation Spectrometer equipped with a radium-226 external standard.

To each radioactive area was added a further 200 μg of carrier steroid and the chromatographic homogeneity of the ^{14}C-compound with carrier steroid was investigated by descending paper chromatography using the following Bush-type systems: benzene:heptane:methanol:water (83:167:200:50) (B_3); heptane–80% methanol (HM-80); heptane:benzene (1:1)–70% methanol (HBM–70); toluene–70% methanol (TM–70); and benzene–50% methanol (BM-50).

Purification of Materials

All solvents were reagent grade and distilled through a Vigreux column with the first fraction (20% of total) and last fraction (2% of total) being discarded. Whatman No. 1 chromatographic paper was washed by descending chromatography with hexane followed by methanol. The washed paper was dried at room temperature and stored in a polyethylene container. The precursors [4–^{14}C] pregnenolone and [4–^{14}C] progesterone were purified by chromatography in the same chromatographic systems as the corpuscles of Stannius extracts.

Location of Steroids

Chromatograms were scanned for ^{14}C using a Nuclear-Chicago 4π Actigraph II chromatogram scanner and location of radioactive areas were compared with the positions of the ultraviolet absorbing carrier steroids.

Acetylation

The dry steroid residue was dissolved in 0.2 ml of anhydrous 20:1 acetic anhydride–pyridine and allowed to stand for 16 hr at 20–25 C. Two milliliters of methanol were added and the solution was evaporated to dryness using nitrogen at 40 C.

Saponification

The steroid acetate was dissolved in 4.0 ml of 0.066 N KOH in 90% ethanol under nitrogen and saponification was allowed to proceed in the dark for 2 hr in a tightly capped 10-ml centrifuge tube. The potassium hydroxide was neutralized using 0.1 N acetic and steroids were extracted from the aqueous solution with three portions of 2.5 volumes of dichloromethane. It was found that the above method would not completely saponify the acetate of 20β-dihydroprogesterone. Saponification of this compound was accomplished as follows: the steroid residue was dissolved in 4 ml of 0.2 N potassium hydroxide in 90% ethanol under nitrogen and left overnight at 57 C. The potassium hydroxide was neutralized with acetic acid immediately after the tube was opened and the steroid was extracted as in the first method.

Preparation of 20β-Dihydro-Derivatives

The reagents were prepared as in the enzymic determination of corticosteroids (Margraf et al., 1963). To 100 μg of 20-oxo-steroid was added 0.6 ml of ethanol, 9.6 ml of 2 parts TRIS buffer (*p*H 7.3) to 1 part glycerine, 0.6 ml $NADH_2$ (5 mg/ml of TRIS) and 0.6 ml of 20β-hydroxysteroid dehydrogenase (5 mg/ml obtained from Boehringer Mannheim Corporation, N. Y.). Reaction was allowed to proceed for 2 hr at 20–25 C when the mixture was diluted to 20 ml with water and extracted three times using 2.5 volumes of dichloromethane. The dichloromethane extracts were combined and flash-evaporated at 40 C. The steroid was isolated by chromatography.

Crystallization to a Constant Specific Activity

Approximately 10 mg of chemically pure standard steroid were added to the chromatographically purified ^{14}C-steroid in a 1-ml glass-stoppered centrifuge tube. The steroid mixture was dissolved in 0.5 ml of boiling acetone on a hot-water bath and water was added dropwise until the hot solution was cloudy. The solution was allowed to stand at room temperature until crystallization was complete. The crystals were centrifuged, supernatant liquid was drawn off, and a small portion of the crystals was removed, placed on a 22-mm square cover slip, and dried to constant weight in a vacuum desiccator over phosphorus pentoxide. The dried crystals were weighed on an aluminum pan of a model G Cahn electrobalance and then washed from the aluminum pan into a counting vial using methanol. Crystallization of the residue remaining from the first crystallization was repeated using the same procedure until the specific activity remained constant for three consecutive recrystallizations.

RESULTS

In the first incubation where [4–^{14}C] progesterone was used as precursor, [4–^{14}C] 11-desoxycorticosterone (DOC) was isolated. Biosynthetic DOC had the same chromatographic mobilities as standard DOC in thin-layer systems 1 and 2, and on paper in the Bush B_3 and HM-80 solvents. When the acetate was prepared, the radioactivity failed to separate from DOC acetate carrier in the HM-80 system. The [4–^{14}C] DOC acetate was saponified and rechromatographed in the HM-80 system where the radioactivity had the same mobility as standard DOC which was run concurrently. 20β-Dihydro-DOC was prepared from the DOC isolated from the saponified DOC acetate. When the 20β-dihydro-DOC was chromatographed on thin layer using the chloroform:methanol:water (90:10:1) system, the radioactivity did not separate from the 20β-dihydro carrier. The yields of DOC acetate and 20β-dihydro-DOC, as a percentage of the total radioactivity recovered from the incubation, were 0.032 and 0.028%, respectively.

In experiments 2 and 3 where [4–^{14}C] pregnenolone was used as precursor, [4–^{14}C] progesterone was isolated. Biosynthesized [4–^{14}C] progesterone was not

separated from cold carrier in the two thin-layer systems nor with HM-80 on paper. The 20β-dihydro-derivative was prepared and chromatographed in the HM-80 system where the radioactivity and standard carrier compound were again homogeneous. The acetate of 20β-dihydroprogesterone was prepared and chromatographed in the HM-80 system where the radioactivity was retained with the carrier. The acetate was saponified and chromatographed in HM-80 and the radioactivity remained with the standard 20β-dihydroprogesterone. In experiment 3, standard 20β-dihydroprogesterone was added to the saponified biosynthesized ^{14}C-steroid. The mixture was recrystallized from an acetone–water mixture and three consecutive specific activities were 523, 534, and 542 dpm/mg. The yield of progesterone relative to total radioactivity recovered from the incubate was 1.02% after isolation in the HM-80 system. On the same basis, the yield of 20β-dihydroprogesterone was 0.75% following chromatography.

In addition to the transformation of the precursors to progesterone and 11-desoxycorticosterone, there was a great deal of transformation of the precursors to several unidentified products. In experiment 1, a compound was isolated that had the same chromatographic mobility as cortisol in ethyl acetate:cyclohexane:toluene (10:10:1) and chloroform:methanol:water (90:10:1) thin-layer systems. Much of the radioactivity remained with cold cortisol carrier during paper chromatography in the TM–70 and BM–50 systems. When the acetates were prepared the unknown ^{14}C-acetate was less polar than cortisol acetate.

DISCUSSION

This investigation demonstrated the presence of 3β-hydroxysteroid dehydrogenase, Δ^5-3-ketosteroid isomerase, and 21-hydroxylase in the corpuscles of Stannius of cod. Progesterone and 11-desoxycorticosterone were the only Δ^4-3-ketosteroids isolated and identified from *in vitro* incubations. The failure to demonstrate 3β-hydroxysteroid dehydrogenase histochemically in the present study suggests that negative histochemical results obtained with other species should be reinvestigated. Chester Jones et al. (1965) have reported the failure of *in vitro* tissue incubations of corpuscles of Stannius of the European eel (*Anguilla anguilla*) to transform pregnenolone and progesterone to 11-desoxycorticosterone, 17α-hydroxyprogesterone, 11-desoxycortisol, corticosterone, cortisone, cortisol, and aldosterone, but reported a slight transformation of added precursors to unidentified products. Phillips and Mulrow (1959) were also unable to detect cortisol, cortisone, corticosterone, or aldosterone when corpuscles of Stannius from the winter flounder (*Pseudopleuronectes americanus*) were incubated with progesterone. They concluded within the limitations of the techniques employed, that the corpuscles of Stannius were not concerned with the production of adrenocorticosteroids. It is of interest to note that both studies where negative results were obtained were done at 37 C while 20–25 C was used in the present investigation. Idler and Truscott (1966b) recently reported that the conversion of corticosterone to

1α-hydroxycorticosterone by interrenal tissue of an elasmobranch (*Raja radiata*) went in good yield from ambient to 30 C but there was no reaction at 37 C. It remains to be determined if this applies to any other transformation of steroids in fish.

Fontaine and Leloup-Hatey (1959) claim to have identified cortisol and corticosterone in the corpuscles of Stannius of the Atlantic salmon (*Salmo salar*) and found that this tissue contained a higher hormone level on a unit weight basis than did the anterior interrenal.[4] Ogawa (1963) obtained a triphenyltetrazolium chloride positive spot in the "desoxycorticosterone zone" during chromatography of extracts prepared from incubations of corpuscles of Stannius from the Japanese goldfish (*Carassius auratus* L.).

Chester Jones et al. (1966) have demonstrated pressor activity in extracts from the corpuscles of Stannius of the European eel and suggest that the corpuscles of Stannius might belong to a renin-angiotensin system analogous to that of mammals. The fall in blood pressure and electrolyte disturbance with the removal of the corpuscles of Stannius is suggestive of mineralocorticoid deficiency (Chester Jones et al., 1966). The correction of these abnormalities by administration of corpuscles of Stannius extracts (Chester Jones et al., 1966) suggests the presence of a hormone substance in the corpuscles. Desoxycorticosterone is a potent mineralocorticoid for mammals and it might be worth examining the eel carefully for the possible presence of this hormone. Although DOC seldom accumulates in tissues and body fluids, there are at least two instances where extremely high concentrations have been reported (Simpson et al., 1963; Schildknecht et al., 1966).

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NOTES

First Record of *Pyrgopsis lemur* (Cephalopoda; Cranchiidae) from the Northwest Atlantic

A single specimen of the cranchiid squid *Pyrgopsis lemur* Berry 1920 was taken on the southern part of the Grand Bank by the M. V. *Blue Foam* on April 25, 1951 (Fig. 1). The specimen was taken by otter trawl at 43°52′N, 49°20′W, at a depth of 36–44 fath (66–81 m).

Characteristics of the specimen agree well with the preliminary diagnosis of Berry (1920). However, Berry's specimen had stouter tentacles (undoubtedly contracted) and the arm formula 3.4 = 2.1.

The mantle is long and slender, expanded near the middle, thence tapering to a narrow point posteriorly. It is thin, fragile, and colorless. Ventrally there are two rows of cartilaginous tubercles which extend posteriorly from the points of attachment of the mantle. These are about $\frac{1}{8}$ the mantle length and consist of a few large spinous tubercles with smaller simple ones between them. The mantle is slightly produced anteriorly at the points of attachment.

The fins are terminal, broader than long, and transversely elliptical. They are widest slightly posterior to their midpoint.

The head is narrow and elongate. It is flattened ventrally and, less so, dorsally. The eyes are on stalks which are almost as long as the head. The funnel extends anteriorly between the eyes.

The arms are in the order 3.2.4.1. The third arms are approximately three times as long as the second and fourth and are much stouter than the other arms or tentacles. The dorsal arms are very short. All the arms have dorsal and ventral protective membranes. On the distal tip of the third right arm these membranes are expanded to form a pair of small flaps. (The tip of the corresponding left arm is missing.) The suckers are biserial and alternate.

The tentacles are long and slender with small, slightly expanded clubs. Dorsal and ventral trabeculate protective membranes are present. There is also a broad swimming membrane on the distal half of the club. The club suckers are in four rows, those of the two medial rows of the manus being about four times as large as the lateral suckers. Distally they diminish in size. There appear to be seven suckers in the carpal cluster and these are arranged in two diagonal rows, the distal one comprising four suckers. Minute suckers are continued in an alternate pattern on the distal half of the tentacle stalk. These are most widely separated proximally.

Measurements of the specimen (as defined by Voss, 1956, 1963) are as follows:

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Mantle length	37.8 mm	Arm I	3.9 mm
Mantle width	10.0 mm	" II	7.5 mm
Fin length	10.4 mm	" III	20.2 mm
Fin width	16.9 mm	" IV	6.0 mm
Head length	10.1 mm	Tentacle length	30.2 mm
Head width	1.8 mm	Club length	4.2 mm

Berry (1920) and Degner (1925) have noted the similarity between this species and *P. schnehageni*. In tabling a comparison of *Pyrgopsis* species, Degner (1925, p. 57) made errors in taking measurements from Berry's figure. As a result, the body proportions he lists for this species are not valid.

This is the third published record of *Pyrgopsis lemur* and the specimen is the largest yet reported. Berry's specimen was taken east of Cape Hatteras at 35°27′N, 73°14′W. Voss (1958) reported a single specimen from 18°43′N, 65°10′W.

Dr W. Templeman critically read the manuscript. The photograph is by Mr E. L. Rowe.

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Received for publication February 4, 1966.

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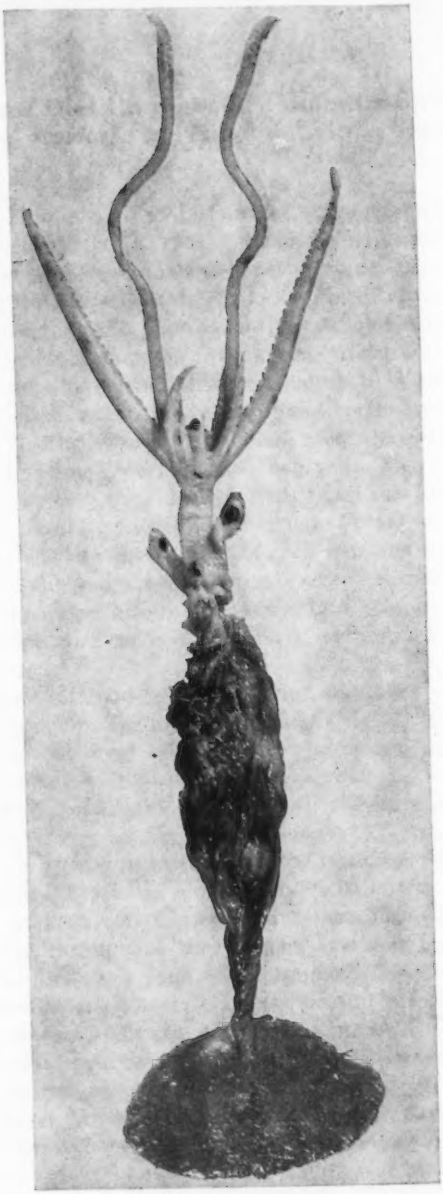

FIG. 1. *Pyrgopsis lemur* (× 2.4), southern Grand Bank, April 25, 1951. (The posterior part of the body is twisted in the photograph.)

Mercer — J. Fish Res. Bd. Canada

Seasonal and Diel Changes in Food of Adult Kokanee (*Oncorhynchus nerka*) in Nicola Lake, British Columbia

As a result of studies on distribution and spawning migration of kokanee in Nicola Lake (Northcote et al., 1964; Lorz and Northcote, 1965), information was obtained on food habits of adult kokanee. Surprisingly enough, there seem to be few cases in the literature where food items of sizable numbers of this species are given in any detail. Consequently results of stomach analyses from kokanee taken in gill net samples from spring to autumn (1959, 1960) and during an intensive 24-hr netting series in August 1963 are summarized here.

The majority of kokanee were taken at the northeast end of Nicola Lake (stations 1 and 2, Northcote et al., 1964) and most were maturing fish in their 3rd year of life. A few fish were in their 4th year (3+) and in the October 1959 sample many were in their 2nd year. Age and size distribution of Nicola Lake kokanee are given by Lorz and Northcote (1965). After preservation in a 10% solution of formalin the content of each stomach was removed, blotted to remove excess liquid, and the total volume was determined by displacement. Food items were separated into major groups in a petri dish using a binocular dissecting microscope, and the contribution of each group to the total volume of food was estimated.

Average volume of food in the kokanee stomachs was highest in June and October but low throughout the summer (Fig. 1). Crustacean plankton formed the bulk of the food taken in the spring and autumn. Diaptomids, largely *Epischura nevadensis* with a few *Diaptomus* sp., were dominant in the spring while *Daphnia* was most important in the autumn. No attempt was made to separate species of *Daphnia*. Brooks (1957) records *D. longiremis*, *D. schødleri*, and *D. thorata* from the lake, the latter species with admixture of a few *schødleri* traits. *Leptodora kindtii* only contributed appreciably to adult kokanee diet in midsummer. Chironomid pupae formed an important food source for kokanee throughout the summer, making up about 70% of the average volume in June and July. Of the pupae, *Chironomus* sp. (possibly *C. plumosus*) and *Procladius* sp. were by far the dominant forms. *Cryptocladopelma* sp. (possibly *C. amachaerus*) was taken occasionally. Chironomid larvae contributed in a minor way to the summer diet. Miscellaneous zooplankters, aquatic and terrestrial insects, and water mites rarely exceeded 1% of the volume at any time. No marked or consistent differences were noted in the food habits of kokanee captured in various regions or depths of the lake.

Information on diel changes in food habits was obtained from stomachs of kokanee taken during daylight and overnight gill net sets (Fig. 2). A higher proportion of diaptomids and *Leptodora* was found in stomachs of kokanee captured during the day compared with those at night. Chironomid larvae contributed more to stomach volume during the day, whereas pupae volumes

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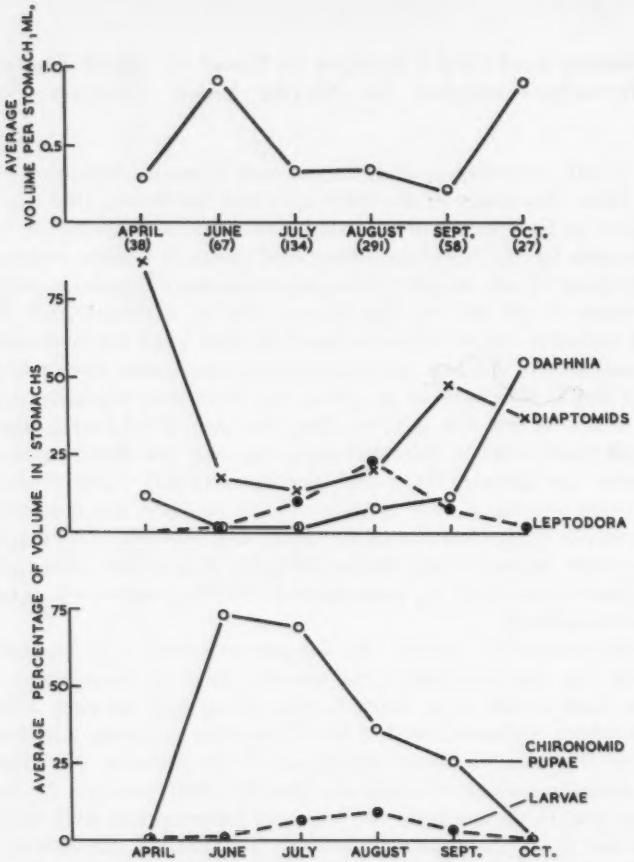

FIG. 1. Seasonal changes in volume and composition of food taken by kokanee from Nicola Lake in June–October 1959 and April 1960. Numbers of fish sampled given in parentheses.

were consistently greater in stomachs of fish taken at night. Later in summer the average volume of food in kokanee stomachs was lower at night than during the day. In the 24–25 August series (Fig. 2) where night samples were divided into three time-periods, a gradual decline in average volume of food was evident through the night. A similar decline was shown more clearly in volume of food in stomachs taken during the diel series in late August 1963 (Fig. 3). Here, too, Leptodora contributed more to stomach volume of kokanee during daylight hours than during the night, whereas chironomid pupae were more important during the night and morning.

A decrease in average volume of food in kokanee stomachs was evident during summer and may be related to approaching maturity prior to entry

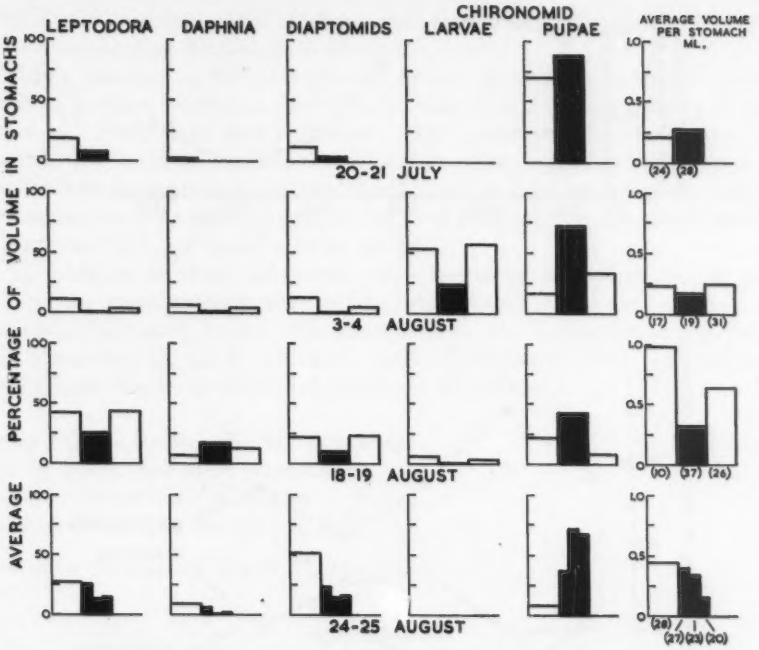

FIG. 2. Changes between day and night in volume and composition of food taken by adult kokanee in Nicola Lake during summer 1959. July and late August histograms show results from fish captured in consecutive-day (open bar) and night (solid bar) net sets; August 3–4 and 18–19 histograms likewise show results from consecutive net sets made during the first day, overnight, and then the following day. Numbers of fish sampled given in parentheses.

into spawning streams which usually began in mid August. Platts (1958) noted an October decrease in food consumption of maturing kokanee in Lake Pend Orielle before spawning started in November–December. A decrease in volume of food consumed with maturity has also been noted in kokanee from Shuswap Lake (J. Goodman, personal communication). Immature Nicola kokanee taken in October (most of which would spawn next autumn) had a much higher average volume of food in their stomachs than did somewhat larger mature fish taken a month before (Fig. 1).

Previous studies (Clemens et al., 1939; Platts, 1958; Chapman and Fortune, 1963; Horak and Tanner, 1964) have noted the importance of crustacean zooplankters in the diet of adult kokanee, with cladocerans such as *Daphnia* and *Bosmina* and copepods such as *Epischura*, *Diaptomus*, or *Cyclops* being usual representatives. Ricker (1937) found that adult residual sockeye in Cultus Lake fed heavily on these same genera of entomostracans and noted that sockeye and kokanee ate identical foods in the lake (Ricker, 1940). Platts (1958) recorded the presence of *Leptodora* in adult kokanee stomachs but no

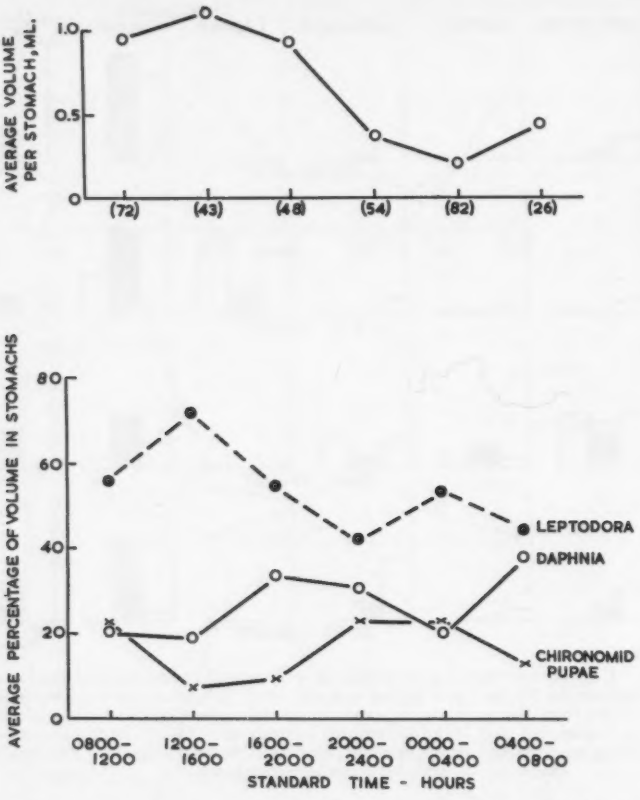

FIG. 3. Diel changes in volume and composition of food taken by adult kokanee in Nicola Lake during 4-hr intervals, August 25–26, 1963. Numbers of fish sampled given in parentheses.

previous studies have indicated the dominance which this large predaceous plankter may have at times in the food of kokanee.

Chironomids have usually been regarded as minor items in the food of adult kokanee (Clemens et al., 1939). In Lake Yunoko, Japan, chironomid larvae were found in 12.1% and pupae in 15.1% of 33 kokanee stomachs examined (Shiraishi and Takagi, 1955), although at times they occurred more frequently. In Nicola Lake, chironomids were a major food component throughout summer, and in some months pupae composed nearly 75% of the diet. Thus, while perhaps primarily a pelagic feeder, the kokanee may derive a significant fraction of its food supply from emerging bottom fauna. Although kokanee in Nicola Lake may be closely associated with the bottom, during the day as well as at night (Northcote et al., 1964), the presence of chironomid larvae in stomachs does not necessarily indicate bottom feeding. Mundie

(1959) found a wide variety of chironomid larvae near the surface of Lac la Ronge at night over depths up to 40 m.

Adult kokanee in Nicola Lake are known to undergo extensive vertical as well as onshore — offshore movements, both with a diel periodicity (Northcote et al., 1964; Lorz and Northcote, 1965), however diel changes in food habits do not seem to be obviously related to these movements. Diel changes noted in the proportion of various food items in kokanee stomachs suggest that caution must be used in interpreting food habits of this fish where samples are restricted to a portion of a 24-hr period.

In addition to those acknowledged in previous studies on Nicola Lake kokanee, the conscientious effort of Mr John Maher in stomach analysis was sincerely appreciated as was the identification of chironomid larvae by Dr A. L. Hamilton. Dr G. F. Hartman, Dr C. C. Lindsey, Miss Jan Goodman, and Mr John Mason gave helpful criticisms and advice.

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Received for publication March 25, 1966.

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A "Red Water" Bloom of *Gonyaulax acatenella* in the Strait of Georgia and its Relation to Paralytic Shellfish Toxicity

Several species of marine dinoflagellates of the genus *Gonyaulax* have been linked with red water occurrences in North America but only a few have been shown to be associated with production of paralytic toxin found in shellfish. To date only *Gonyaulax catenella* and *Gonyaulax tamarensis* have been established as the primary sources of toxin in shellfish on the Pacific and Atlantic coasts, respectively (Sommer et al., 1937; Prakash, 1963). Toxin has also been reported in *G. polyedra* (Schradie and Bliss, 1962) and there is reason to believe that this organism may be associated with paralytic shellfish poison in southern California coastal waters. *Gonyaulax monilata*, frequently the cause of red water blooms in the Gulf of Mexico, was implicated with toxicity to fish (Gates and Wilson, 1960), but an association with shellfish toxicity has yet to be established. The present report deals with yet another species, *Gonyaulax acatenella* Whedon and Kofoid, which was responsible for red water blooms in the Strait of Georgia and was found to be the source of toxin in shellfish.

In 1965, an outbreak of paralytic shellfish poisoning occurred in the Strait of Georgia in British Columbia. All the cases reported were from the northeastern part of the Strait in the Malaspina Inlet area and included one fatality and four known illnesses. In each case, the symptomology was typical of paralytic shellfish poisoning (McFarren et al., 1960). The single fatality was reported on the night of May 31, 1965, and involved an elderly man who had eaten a meal of cockles at midday. The medical officer who performed the autopsy found a large number of cockles in the patient's duodenum and attributed the death to toxin from shellfish. The cockles (*Clinocardium nuttallii*) had been dug from a beach at the entrance to Theodosia Inlet off the Malaspina Inlet (Fig. 1) and were cooked before eating. Four other persons who shared the same meal became violently ill but recovered and were discharged from the hospital within 2 days. Another case of mild poisoning was reported in the same week from Myrtle Point south of Powell River but no details were available.

In the first week of June, several people in the area near Malaspina Inlet reported observing red water patches and intense phosphorescence in the water at night. On June 3, 1965, the medical health officer at Powell River reported sighting large patches of deep red or maroon-coloured water while flying over Okeover, Lancelot, and Theodosia inlets. Samples of red water and plankton were collected from these locations during the same week and brought in preserved and fresh condition to the Nanaimo laboratories of the Fisheries Research Board of Canada for examination. Plankton samples revealed that the discolouration in Theodosia and adjacent inlets was due to an extensive bloom

J. Fish. Res. Bd. Canada, 23(8), 1966.
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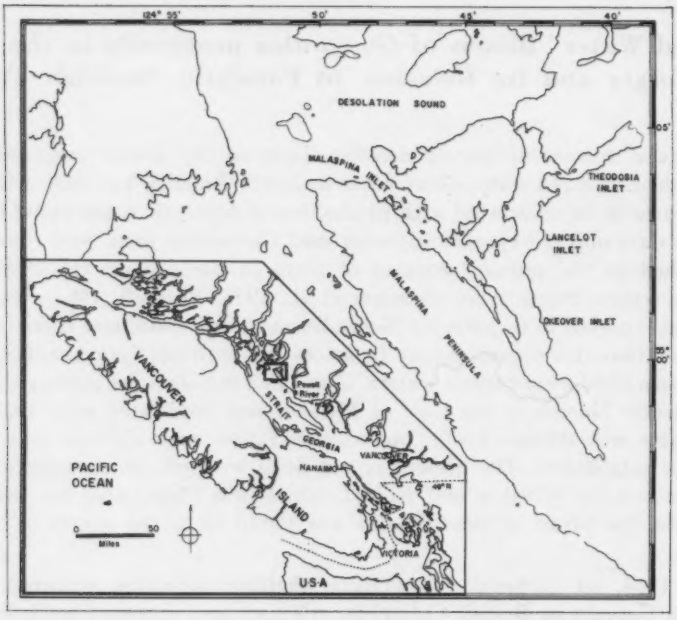

FIG. 1. Malaspina Inlet complex in the Strait of Georgia.

of a dinoflagellate species identified as *Gonyaulax acatenella* Whedon and Kofoid (Fig. 2).

Gonyaulax acatenella resembles *G. tamarensis* of the Atlantic waters in size, shape, and arrangements of plates and shares some common features with an allied species *G. catenella* found along the Pacific coast from California to Alaska. The specimens of *G. acatenella* were distinguished from these two species by virtue of the general shape of the cells, size and shape of the apical plates, lack of a curtain fin on the girdle, and lack of a posterior attachment pore. Figure 2a shows a ventral view of an empty theca of characteristic size and shape. Figure 2b also shows an empty theca of a larger cell in which the naked protoplast appears to have escaped laterally just above the girdle. In Fig. 2c the cells are densely packed with chromatophores that range in colour from a pinkish-orange to a red-brown. Apart from chromatophore content, the cells conformed closely with Whedon and Kofoid's (1936) original description of *G. acatenella*. The size and shape of the plates in the ventral region was found to be too variable to warrant the systematic significance placed on them by the original authors.

The bloom was almost monospecific with very insignificant representation of other species of phytoplankton. *Gonyaulax acatenella* was in an active phase of growth in the red water samples and chains of 4–6 individuals were frequently

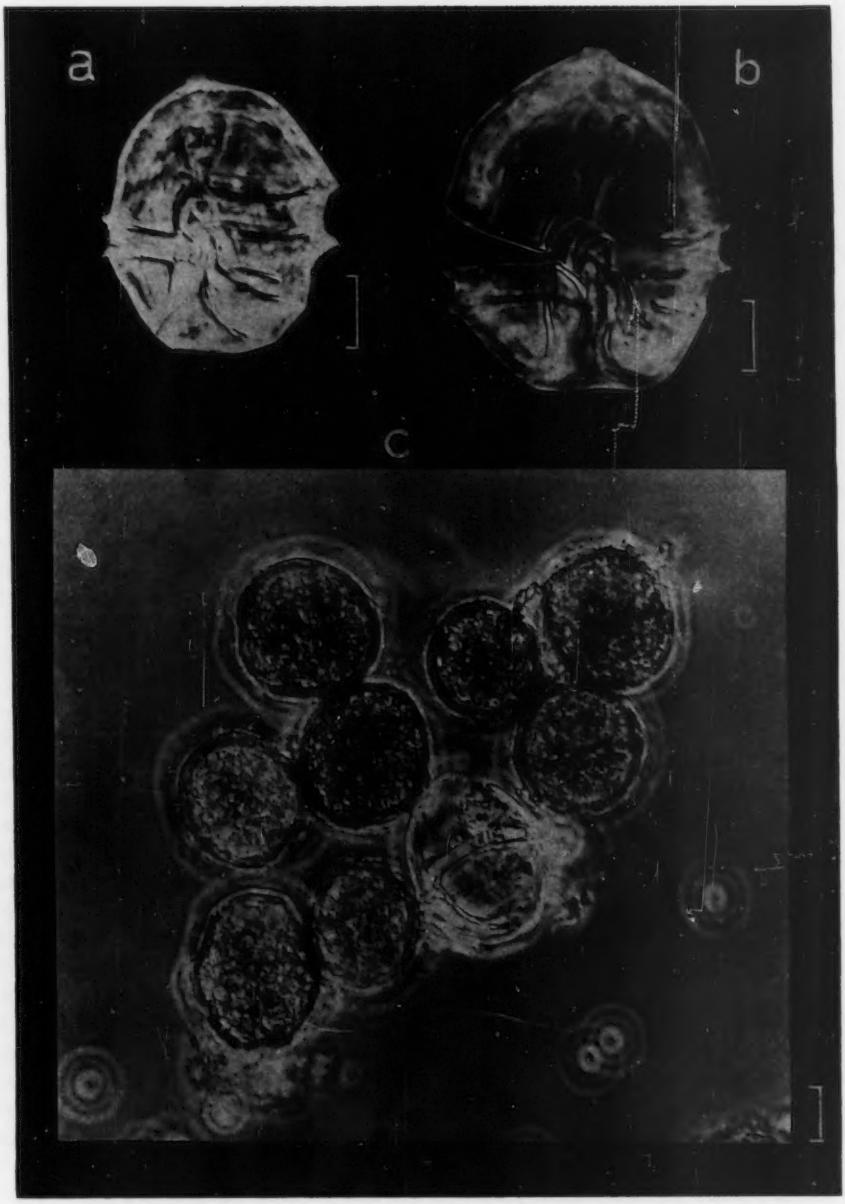

FIG. 2. *Gonyaulax acatenella* from Theodosia Inlet. a and b. ventral view of empty thecae; c. typical appearance of the cells at the time of the bloom. Scale line represents 10 μ.

observed swimming about. Each cell was strongly pigmented, packed with chromatophores ranging from pinkish-orange to reddish-brown in colour. Counts of *Gonyaulax* in the red water samples were made using Utermöhl's sedimentation method and cell densities as high as 13.5×10^6 cells per litre of sea water were estimated. This concentration imparted a red or rusty hue to sea water under ordinary light conditions. Other phytoplankton organisms associated with the *G. acatenella* bloom included the diatom *Nitzschia delicatula* and a few other dinoflagellate species (*Peridinium conicum*, *P. conicoides*, *P. oblongum*, *P. steinii*, *Phalacroma irregulare*, and *Ceratium* sp.). Of these, *Nitzschia delicatula* was the commonest. Zooplankton were represented only by a few adult and juvenile copepods and the tintinnid *Helicostomella subulata* in the red water patches.

Hydrographic and meteorological observations made during and after the peak of the bloom revealed that the conditions for development of the *G. acatenella* bloom were more favourable in Theodosia, Lancelot, and Okeover inlets than in outside waters. These inlets showed marked vertical stability and the temperature profiles were generally similar. After the peak of dinoflagellate bloom, however, no significant differences in temperatures between inlet waters and outside waters were detectable. Microbiological assays for vitamin B_{12} in filtered red-water samples collected from Theodosia Inlet on June 11, 1965, revealed concentrations as high as 13.0 mμg/liter (T.R. Parsons, personal communication) and it is likely that this high level of vitamin B_{12} might have triggered the dinoflagellate bloom in the Malaspina Inlet area. There is an impressive body of data which has shown a specific B_{12} requirement in a large number of marine dinoflagellates and has recognized this vitamin as one of the metabolites governing algal blooms (Provasoli, 1958). During the period that the red-water blooms were noticed in the various inlets of the Malaspina complex, the weather was generally calm and the light conditions extremely good. Sunshine records obtained from Nanaimo, Cowichan Bay, and Vancouver Airport revealed that the sunshine amounts in May and June 1965 were substantially higher than normal. In fact, the June total was a new record high accumulation of sunshine with the period of record going back to 1947. May and June solar radiation data for 1964 and 1965 collected at Nanaimo showed much higher values for 1965 and specially during the first week of June when the red-water bloom was at its peak development. Total radiation value on May 31, 1965, was 776 g-cal/cm^2 /day and averaged 748 g-cal/cm^2/day between June 1 and June 9. Radiation values during 1 week preceding and 1 week following the red-water bloom peak were considerably lower and averaged 589 and 600 g-cal/cm^2/day, respectively. These figures may be regarded as representative of conditions in the entire Strait of Georgia.

In order to estimate the toxicity of *G. acatenella*, cells were harvested from a known volume of red water by millipore filtration and their extracts prepared according to methods developed for *G. tamarensis* by Prakash (1963). The bioassays revealed toxin in *G. acatenella* cells and scores as high as 0.46 μg or approximately 3 mouse units per millilitre of extract were recorded. Toxin

yield from 13.5×10^5 cells was calculated to be 225 mouse units or one mouse unit per 6000 cells, indicating a poison load per cell in *G. acatenella* high enough to make shellfish feeding on them toxic for human consumption. *Gonyaulax acatenella* has never been linked with the production of toxin; the present report appears to be the first instance where this species has been implicated.

In Whedon and Kofoid's description of *G. acatenella* particular note was made that the cell contents were colourless to greenish, with few starch granules, few chromatophores, and a few oil droplets. Sommer et al. (1937) grouped *G. acatenella* with apparently nontoxic dinoflagellates showing no marked colour change and tentatively suggested that as colour variations are indicative of physiological changes in the cell, they might be related to the occurrence of toxin. Mention has already been made of strong pigmentation in *G. acatenella* cells during the red-water bloom in Malaspina Inlet and high toxicity in this species. While colour is not normally considered of much significance in dinoflagellate taxonomy since it is known to vary with light intensity and age of individuals (Bursa, 1959; Silva, 1962), it is rather interesting in the present case where a species of *Gonyaulax* normally considered nontoxic in a colourless or weakly pigmented state was found to be toxic in a highly pigmented state. Attempts to culture *G. acatenella* in the laboratory were not successful and therefore a comparison of the highly and weakly pigmented populations of this species with respect to toxicity variations could not be undertaken. There is of course also the possibility that *G. acatenella* and *G. catenella* are conspecific, since one of us (F.J.R.T.) has observed chains of *G. catenella* from the Puget Sound area in which some of the cells closely resembled the Theodosia Inlet specimens of *G. acatenella* in size and shape but not in the plate arrangement. This possibility is further strengthened by the observations made by Braarud (1951) on morphological variability in cultures of *G. tamarensis* and also the apparent existence of toxic and nontoxic strains of the same species in different geographical locations (Prakash, 1963).

No records of shellfish toxicity in Malaspina Inlet area prior to 1965 summer outbreak are available. The first bioassay for shellfish toxicity in that area was made on May 31, 1965, soon after the reports of poisonings became known. Extracts of leftover cooked cockles (*Clinocardium nuttallii*) dug by the affected family from Theodosia Inlet were prepared and sent to the Laboratory of Hygiene, Ottawa, for bioassay. Results indicate up to 1920 μg or about 12,000 mouse units of toxin per 100 g of shellfish meat. This is sufficient toxin to cause severe poisoning depending upon the quantity of toxic shellfish consumed (Medcof et al., 1947). No accurate estimates of the quantity of toxic shellfish consumed could be made but not less than 12,000 mouse units were likely ingested by each affected individual. Raw butter clams (*Saxidomus giganteus*) dug on June 1, 1965, in the area where toxic cockles were obtained showed a toxicity level of 3840 μg or 24,000 mouse units. Other species of shellfish in which toxin was detected in the Malaspina Inlet area included Manila clam (*Venerupis japonica*), native little neck clam (*Protothaca staminea*), soft-shell clam (*Mya arenaria*), horse clam (*Tresus*

capax), bay mussel (*Mytilus edulis*), and Pacific oyster (*Crassostrea gigas*) (Table I). Most shellfish species recorded higher toxicity scores during the first 2 weeks of June than later in the season. This coincides with the period when the *G. acatenella* bloom was most developed in the Malaspina Inlet area. Of all species, butter clam retained the toxin longest, natural detoxification being extremely slow. Most of the poison in toxic butter clams was concentrated in the siphon. Pacific oysters, on the other hand, became toxic only during the red tide bloom and lost their toxicity almost completely by the end of June. Shellfish sampled from locations where no red water bloom was observed showed little or no toxicity during the same period. There is thus sufficient evidence to link the sudden rise in shellfish toxicity in the Malaspina Inlet area with the occurrence of the red-water bloom caused by *G. acatenella*.

TABLE I. Toxicity levels (in micrograms of toxin per 100 g of shellfish meat) in the various species of shellfish in Theodosia Inlet during and after the red-water bloom in 1965 (the dash indicates no sample available).

Date	Butter clam	Bay mussel	Horse clam	Manila clam	Native clam	Soft-shell clam	Oyster
Theodosia Inlet							
June 1	3840	–	–	–	–	–	–
June 5	8640	4040	3520	1376	1424	240	–
June 16	–	–	–	–	–	–	86
July 12	624	69	192	38	43	–	<32
July 28	1104	42	–	–	–	<32	<32
August 25	1344	38	72	<32	<32	<32	<32

	Butter clam	Cockle	Manila clam	Native clam	Soft-shell clam	Oyster
Lancelot and Okeover inlets						
June 9	–	–	912	–	–	–
June 11	–	–	–	–	–	272
June 15	1920	192	–	288	864	88
July 12	1552	83	–	86	34	<32
July 28	1312	54	–	–	–	<32
August 25	1152	61	<32	37	–	<32

Although outbreaks of paralytic shellfish poisoning due to human consumption of toxic shellfish are not uncommon on the British Columbia coast, the 1965 outbreak is of particular interest not only because of its severity, but also due to the so called "red tide" phenomenon that accompanied it. It was the first outbreak involving human fatality in British Columbia since 1942. In 1942, three persons lost their lives after eating clams in Barkley Sound on the west coast of Vancouver Island and three fatalities were reported from Port Angeles, Washington, in Juan de Fuca Strait (Edwards, 1956). An outbreak of shellfish toxicity also occurred in October 1957 in the Strait of Georgia

which involved over 60 persons but no deaths were reported. A few scattered reports indicate that the 1957 outbreak in British Columbia was either accompanied or preceded by the development of red water in the areas where toxic shellfish were taken. At that time no attempt was made to examine the red water and to identify the causative organism. It is also of interest to note that the 1957 outbreak in the Strait of Georgia was preceded by a long period of intense sunshine and relatively calm weather (Anderson, 1958; Waldichuk, 1958).

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Received for publication January 19, 1966.

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A Portable Aquarium for Use at Sea to Photograph Fish and Aquatic Life

Fisheries biologists and zoologists have the problem of obtaining accurate color or black-and-white pictures of fish and aquatic life. Photographs appear to be the best method of obtaining a realistic record of a live or dead aquatic animal in the field. Existing photographic methods (David, 1963; Ronholt, 1963; Van den Nieuwenhuizen, 1964) were incorporated with the best features of many aquarium designs tested by the author at the Vancouver Public Aquarium. The final design was tested during regular groundfish cruises of the research vessel *G. B. Reed.*

A narrow glass aquarium with an adjustable wedge-shape insert (Fig. 2) and accessory photographic equipment was designed to meet the following requirements: (1) specimen to be photographed alive in water (aquarium) to preserve color and detail; (2) a rapid, moderately inexpensive technique needing only one operator; (3) Portable, sturdy, noncorrosive, and vibration-resistant equipment for use on board vessels in rough seas, or in field camps and laboratories; (4) A constant light source: to illuminate all areas of the specimen, suitable for daylight color film and extra fine-grain slow-film speed black-and-white film; (5) an illuminated changeable white or colored background to accentuate the fins or fleshy appendages of specimens, yet remove all background shadows; (6) a method to spread fins and immobilize the specimen, yet keep natural coloration and shape; (7) circulating filtered water in the aquarium to keep bubbles from the glass surfaces and to provide clear water.

The size of the aquarium depends on the size of fish to be photographed, the ceiling height of the vessel or building, and the height of the photographer. The aquarium weighs 50 lb when empty, occupies a space 36 inches by 30 inches by 7 ft and needs an 8-ft space in front of it for maneuvering. The aquarium and accessories are drawn to scale in Fig. 1 and a diagrammatic cross-section of assembled equipment is shown in Fig. 2. Detailed three-elevation drawings of the aquarium may be obtained from the Fisheries Research Board of Canada, Nanaimo, B.C. To hold the aquarium in place on board ship holes were drilled in the top of the aquarium for rope lashings, or braces can be secured to the support box and aquarium and bolted to the ship's side.

Waterproof plywood was used in most of the aquarium and support box construction. The aquarium was painted with nontoxic matt black paint to prevent reflections. A silicon rubber sealant was used to adhere the glass to the wooden frame.

Filtered water enters at the bottom of the aquarium and is drained off at the top. A 5-μ water filter (Cune Engineering Corporation Model P10) or a diatomaceous earth filter removes particles from the water and the circulating water prevents gas bubbles from forming on the glass surfaces. Specimens in circulating water usually remain anaesthetized for 5 min. If longer

J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

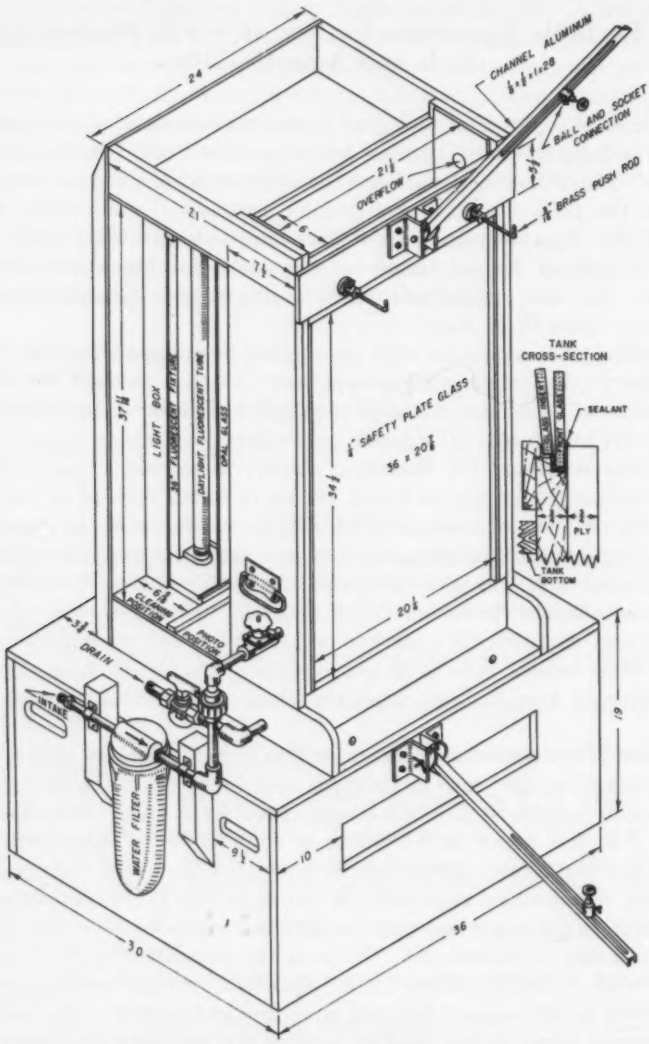

FIG. 1. Scale drawing of the photographic aquarium and accessory equipment (measurements in inches).

time is needed, the anaesthetic should be placed directly in the water, which then cannot be circulated. Bubbles form from uncirculated water; these can be removed from the glass at intervals with scrapers.

Six fluorescent tubes mounted behind double-flashed opal glass produces an even light of high intensity. The light box, which is a separate unit, fits into grooves behind the aquarium. The light box has two mounting positions,

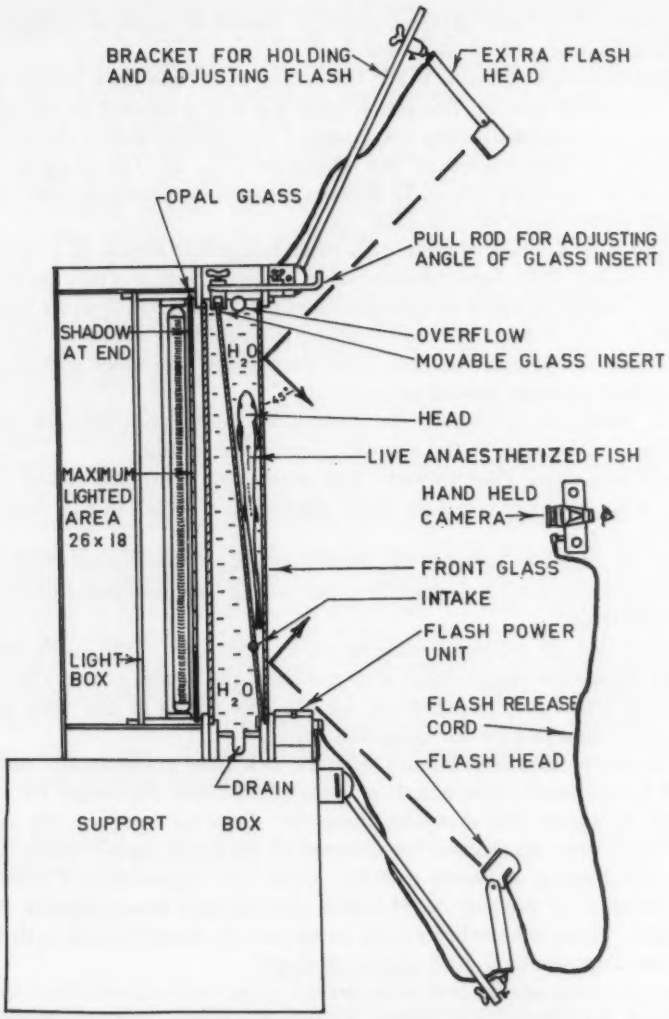

FIG. 2. Diagrammatic cross-section of the photographic aquarium to show the position and function of the component parts.

one for photographing and the other for cleaning the back surfaces of the aquarium glass (Fig. 1, 2). A lighted area 12 by 26 inches is produced by the front light (Fig. 2). Larger fish up to 34 inches may be photographed although the background may appear darker at the extremities. Daylight fluorescent tubes produce a near white background while warm tubes produce a pinkish effect and cool tubes a bluish background. Opal plastic sheets, translucent

vinyl plastic, or colored gelatine may be placed in front or behind the opal glass for a background of any color.

Electronic flash (Braun F 80, 160 w/sec with twin flash heads) was used for the front light source. The power pack fits into a bracket at the side of the aquarium and the flash heads are attached to ball-and-socket connectors that slide along the flash holders of the aquarium (Fig. 2). The angle of the flash is directed at the aquarium at 45 degrees to prevent reflections and yet obtain maximum penetration of light (Fig. 2).

A single-lens reflex camera with interchangeable lenses of 35 or 120 film size was chosen. Twin-lens cameras have proven unsatisfactory at sea. Ultra-fine grain black-and-white 35-mm produces grainless 8 × 10 prints but a larger film size (4 × 5 or 8 × 10) is advisable for large color prints or book plates. Macro lenses for 35-mm cameras allow very small and large specimens to be photographed without special adaptation.

It is better to hand-hold the camera on board ship because of lack of floor space and because of the hazard of excessive motion.

Black and white Panchromatic film with extra fine grain and in the range of ASA 25 to 80 is preferred for good definition in larger prints, from 35-mm or 120-film.

Color film can be selected by photographing a color separation and grey scale card (7-inch size) mounted in clear plastic and immersed in the photographic aquarium.

Comparison of transparencies or color prints with the color separation card will determine which color film produces the truest color. The addition of warming filters may compensate for the cool colors in the flash light and for the color absorbed by the glass and water.

A 45 degree angle set square with 24-inch base constructed from $\frac{1}{4}$-inch plywood (waterproof), fiberboard, or clear plastic sets the angle for the flash units and measures the distance along the diagonal between the specimen and the aquarium. An electric fan directed at the front glass reduces the problem of glass fogging in warm weather. Fish were anaesthetized either by 2-phenoxyethanol (2 ml/gal) or M.S.222 (tricaine methanesulfonate, 1 g/gal) (Bell, 1964). Many invertebrates can be relaxed or anaesthetized with 20–30% magnesium sulphate or 5–10% chloral hydrate.

Dust particles are flushed with filtered water and drained from the aquarium before the specimen is added. The F-stop of the camera should be set according to the test-exposure results for the particular film used. The background light color is selected to highlight the specimen.

Live specimens are kept in water immediately upon capture and later transferred to the anaesthetic. 2-Phenoxyethanol produces tetany of the fin and spine erector muscles (especially of sebastids and salmonids), thus enhancing the specimen for photographs. However, the fin-raising effect is not produced in all species of fish. Although M.S.222 does not raise fins, it has the advantage of not producing any violent muscular movements which might damage the specimen, as the anaesthetic takes effect. Good fin shape has

been obtained by applying concentrated 2-phenoxyethanol (under each operculum) with an eye dropper while the fish is held in the normal anaesthetic solution. Rockfish (*Sebastodes*) and other physoclistous fish should have air removed from distended swimbladders and eye sinuses (Gotshall, 1964) using an 18-gauge, ½-inch hypodermic needle.

The angle of the glass insert is adjusted so that the specimen is suspended in the middle of the aquarium and forced against the front glass. Fish are placed in a vertical position with the head up and the ventral surface of the specimen to the left side of the aquarium (Fig. 2). Specimens that float are submerged with a long-handled device shaped like a tuning fork, then the glass insert is tightened to hold the specimen in place. A transparent plastic scale (.005 mm thick) is attached to the front glass. A printed identification number or name is placed under the scale so it may be removed easily by cropping the finished print.

The light box is turned on preferably with a foot switch and the room lights turned off before the film is exposed. Three exposures are recommended with refocusing on different parts of the specimen. A separate exposure should be taken of the color-control card in the aquarium with each roll of film to check exposures and to aid in printing. If the room lights are not turned off, a black card or sheet with a hole for the camera lens must be held in front of the camera to prevent reflections from objects in front of the aquarium.

Appreciation is extended to the following for their help concerning the apparatus and manuscript: G.R. Bell, P.A. Larkin, D.B. Quayle, F.H. Taylor, F. Bernard, C. Morley, H. Selander, S.J. Westrheim, and the shop craftsmen of the Nanaimo Biological Station; Peter Ryan, Dept. of Fisheries; Keith Sandercock, Institute of Fisheries, University of British Columbia; Roger Kerkhan, B.C. Dept. of Education; M. Newman and staff for facilities at the Vancouver Public Aquarium.

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Received for publication February 18, 1966.

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Rare Marine Fishes from British Columbia with First Records of Silver Perch, *Hyperprosopon ellipticum*, and Shanny, *Leptoclinus maculatus*

Since the publication of Clemens and Wilby's (1961) work, several fishes previously unknown from British Columbia have been recorded. These include the night smelt, *Spirinchus starksi* (recorded by McAllister in Dryfoos, 1961); *Bathylagus ochotensis* (McAllister, 1961); *Nansenia candida* (McAllister, 1961); Greenland halibut, *Reinhardtius hippoglossoides* (Westrheim and Pletcher, 1966); topsmelt, *Atherinops affinis* (Peden and Stewart, 1964); widow rockfish, *Sebastodes entomelas* (McAllister and Westrheim, 1965); chilipepper, *S. goodei* (Westrheim, 1965); silvergray rockfish, *S. brevispinis* (Westrheim, 1964); shortbelly rockfish, *S. jordani* (Westrheim and Pletcher, 1966); dusky sculpin, *Icelinus burchami* (Barraclough and Butler, 1965); Puget Sound sculpin, *Artedius meanyi* (Rosenblatt and Wilkie, 1963); thornback sculpin, *Paricelinus hopliticus* (Barraclough and Ketchen, 1963); slimy snailfish, *Liparis mucosus* (Peden, 1966); slender cockscomb, *Anoplarchus insignis* (Peden, 1966); longfin gunnel, *Pholis clemensi* (Rosenblatt, 1964); red gunnel, *P. schultzi* (Peden, 1966); Pacific soft pout, *Melanostigma pammelas* (Grinols, MS); and twoline eelpout, *Bothrocara brunneum* (Westrheim and Pletcher, 1966).

This note adds two species to this list as well as comments on the distribution of another two fishes rarely known from British Columbia. In the following accounts, "BC" designates collections deposited in the Institute of Fisheries and "NMC" indicates specimens deposited in the National Museum of Canada. The measurements for *Leptoclinus* are expressed as hundredths of the standard length.

Hyperprosopon ellipticum (Gibbons) Silver surfperch

Eighteen specimens of the embiotocid *Hyperprosopon ellipticum*, ranging between 66 and 78 mm in standard length, were taken on November 15, 1964, near a rocky point by Schooner Cove. This is located at the north end of Long Beach near Tofino. The specimens were captured over a sandy bottom that was between 8 and 10 ft below the intertidal zone. The shore consisted of steeply sloping rock and had large dense beds of tall eelgrass (*Phyllospadix*). The area was characterized by a strong surge from the open ocean and heavy surf occurred further down the beach. Tarp (1952) records *H. ellipticum* from as far north as Clallum County, Washington. Therefore, these specimens from British Columbia represent a northern extension of the known range for *H. ellipticum*. The specimens are catalogued as BC64-463.

Hyperprosopon ellipticum has colourless pelvic fins and 17 or 18 gill rakers on the lower portion of the first gill arch. This readily distinguishes this species from *H. argenteum*, also known from British Columbia (Clemens and Wilby, 1961), which has 20 or more gill rakers and black pelvic fins.

J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

Hemilepidotus spinosus (Ayres) Brown Irish lord

Clemens and Wilby (1961) report only one specimen of the cottid *Hemilepidotus spinosus* from British Columbia. This specimen, from near Nootka, also represented the northern limit of the known range for this species; however, specimens have been taken near Sooke, Sidney Inlet, Burnsby Island, Cape Scott, and Rose Harbour. The author obtained six larger specimens (BC65-125) at Ucluelet, by diving and using fish toxicant, on February 12, 1965. They were taken amongst rocks overgrown with pink calcareous algae, at a depth of 15–30 ft below the intertidal zone, in an area influenced by wave surge from the open ocean. Pelagic postlarvae, 20–24 mm in standard length, have also been taken near the surface at 51°N and 130°W (BC60-170). Dr D. E. McAllister kindly provided a specimen (NMC61-159) for examination which he obtained with a gill net in 240 ft of water on July 25, 1961, from Puffin Bay, 50 miles south of Sitka, Alaska. This specimen, 149 mm in standard length, provides a considerable northern extension of the known range and the first known occurrence in Alaskan waters. *Hemilepidotus spinosus* is more common than was previously supposed on the exposed coast of British Columbia.

Leptoclinus maculatus (Fries) Shanny

Since this species is known from Washington (Chapman and DeLacey, 1933) and Alaska (Jordan and Evermann, 1898), this first recorded occurrence from British Columbia was readily anticipated. On May 19, 1963, Dr Richard H. Rosenblatt and Mr Gary McTaggart-Cowan secured 40 specimens, ranging between 72 and 129 mm in standard length, while using an otter trawl at a depth of 180–300 ft, over a hard sandy bottom, near the north end of Malcolm Island, Queen Charlotte Strait. These specimens are catalogued in the museum of the Institute of Fisheries as BC63–775. Their counts and measurements are similar to those reported by Chapman and DeLacey (1933).

Andriashev (1954) recognizes *L. maculatus maculatus* as an Atlantic form and *L. m. diaphanocarus* (Schmidt) as a Pacific form. The lower counts appear to identify British Columbia specimens with the Atlantic form. Because of this discrepancy, these specimens are not given subspecific designation here. Twelve of the specimens from British Columbia have the following counts and measurements: — Dorsal spines 58.5 (57–60). Anal spines 1.6 (1–2), soft anal rays 34.7 (34–36). Pectoral rays 15.2 (14–16). Body depth 8.6 (7.7–9.3). Body width behind pectorals 4.4 (3.8–5.2). Head length 19.0 (16.4–20.1). Eye diameter 5.1 (4.7–5.6). Snout length 3.9 (3.6–4.2). Predorsal length 17.2 (16.9–18.6). Preanal length 48.7 (45.7–52.3). Length of pectoral fin 18.0 (15.1–20.7). Length of pelvic fin 8.5 (7.2–9.3).

Rimicola muscarum (Meek and Pierson) Kelp clingfish

Only half a dozen specimens of *Rimicola muscarum* are known from British Columbia (Clemens and Wilby, 1961; Krejsa, 1964). On May 14, 1963, Dr Robert R. Parker of the Fisheries Research Board of Canada obtained 14 specimens (BC63-127) in a beach seine from Whidbey Point, Fitz Hugh Sound,

which is adjacent to Queen Charlotte Sound. During low tide the author obtained 69 specimens (BC65-127) in three hauls of a small beach seine through scattered eelgrass (*Zostera*), at a depth of about 3 ft, near Little Beach, Ucluelet, on March 4, 1965. However, exhaustive seining at the same location during low tide on August 1, 1965, did not uncover additional specimens. Dr D. E. McAllister writes that he has "identified a specimen which was collected from the south beach, Goose Island, British Columbia (NMC65-38) amongst *Zostera* and rock algae; over a fine shell, sand, stone, and rock bottom; and in water at 14°C. and salinity of 30‰. The specimen was taken by E. L. Bousfield on August 6, 1954." This record extends the known range of *R. muscarum* 220 miles northward.

Messrs J. M. Green, D. W. Hagen, W. Low, and E. E. Moodie of the University of British Columbia assisted in collecting most of the specimens reported here. Criticism and advice were offered by Drs C. C. Lindsey and N. J. Wilimovsky of the Institute of Fisheries, Dr D. E. McAllister of the National Museum of Canada, and Mr R. B. Grinols of the U.S. Bureau of Commercial Fisheries.

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Received for publication December 16, 1965.

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Thermal Resistance of Bacteria Isolated from a Heat Processed Fish Product

Nonspore-forming bacteria which have been reported as heat-resistant in certain substrates are considered to be of negligible significance in the bacterial spoilage of heat-processed canned foods and in outbreaks of food poisoning from such products. As reported by Hansen and Riemann (1963), bacteria which are normally not heat-resistant can frequently be isolated from sound canned foods which have been processed in an autoclave. Micrococci isolated from heat-processed fatty products were observed at times during thermal resistance trials to have a greater heat resistance than bacterial test spores (Yesair et al., 1946); studies on these heat-resistant micrococci indicated that the resistance is due not to the inherent resistance of the cells but rather to protection afforded by the nature of the substrate (fat, protein, etc.).

This note presents information on the isolation, thermal resistance, and cultural characteristics of bacteria isolated from commercially heat-processed fish spreads. Major constituents of the spreads were minced fish, a spice–flour formulation, and oil at an average concentration of 9%. The product was heat-processed in 4-oz cans and 2.5-oz jars at 116.6 C (242 F) for 65, 70, or 85 min.

To ascertain the extent of nonsterility in heat-processed spreads, samples from incubated and nonincubated cans and jars were aseptically pipetted or inoculated with sterile cotton buds into tubes of reinforced clostridial medium (RCM) (Oxoid); in all trials incubation was carried out anaerobically at 35 C for varying periods up to a maximum of 1 month. Since the inoculated tubes of RCM contained a large percentage of fish spread inoculum, subcultures were made from tubes not showing growth as well as from those showing positive growth; it was thought that cell multiplication might be inhibited by entrapment of cells within oil phases in the spread-broth substrate. Factors (fat, protein, etc.) which act to protect organisms during heat-processing may also act to prevent their subsequent growth in a processed product (Yesair et al., 1946).

Two types of bacteria were isolated from the heat-processed spreads; the predominant type was a Gram-positive "Chinese letter" (CL) rod form (Skerman, 1959 — p. 111, *Corynebacterium*) with cell sizes of 1–3μ by 0.5–0.6μ. A photomicrograph of a methylene blue stained preparation of this isolate (Fig. 1A) shows the type of cell aggregation which occurred in cultures grown either in broth or on agar. The other types of bacteria present were coccoid forms which were isolated from a very small percentage of spread samples; the coccoid forms were not studied as extensively as the rod forms. Micrococic and CL types were isolated by N. Neufeld (Dept. of Fisheries of Canada, personal communication, 1965) from similar fish spreads and also from one

J. Fish. Res. Bd. Canada, 23(8), 1966.
Printed in Canada.

lot of spread which had been processed at 116.6 C for 70 min and subsequently reprocessed under the same conditions.

The results of a bacterial survey which was carried out to ascertain the source of bacterial types in the spread revealed that the spice–flour formulation contained CL and coccoid forms of bacteria morphologically similar to those isolated from heat-processed fish spreads. A photomicrograph (Fig. 1B) of a methylene blue stained preparation of CL forms isolated from the spice–flour formulation shows cell aggregations similar to those in cultures of fish spread isolates (Fig. 1A). It has been reported that spices are heavily contaminated with bacteria (Castell, 1944; Yesair and Williams, 1942). Although CL and coccoid forms were found in two of the individual constituents of the spice–flour formulation, flour and salt, respectively, evidence was not obtained to indicate whether these bacterial types were actual contaminants of the original products or contaminants from some source within the processing area.

During thermal-resistance studies on CL forms isolated from fish spread and spice-flour formulation, survival of isolates at a certain temperature and over a given time interval was regarded as positive when growth following incubation was observed in at least two out of four replicate tubes either of original heated inoculated substrate or of broth subcultures from heated inoculated fish-spread samples. A 48–72-hr RCM culture of each isolate was used to inoculate sterile fish-spread samples and tubes of RCM. Since the CL isolates were found to form cell aggregates in broth, sterile glass beads were used in an attempt to obtain an even distribution of cells in broth for use as inoculum. The number of bacteria in the inoculated substrates was approximately 6×10^6 cells per millilitre or gram. A Tala syringe (bakery syringe) was used to transfer 2–4 g of inoculated spreads to test tubes (16 × 150 mm) and screw-cap specimen vials (15 × 45 mm); thermal-resistance tests with inoculated spreads were carried out in a water or oil bath using test tubes at temperatures of 80 and 90 C and vials at a temperature of 100 C. Inoculated substrates were held at each temperature for 5, 15, 30, 45, and 60 min subsequent to a heat penetration time allowance for the slowest-heating portion of substrates to reach the required temperature. The tests on one typical CL form isolated from fish spréad (Table I) indicate that, under these experimental conditions, oil or other constituents of fish spread act to protect bacterial cells from heat inactivation. Similar results were obtained with CL form isolates from the spice–flour formulation. Protection was also afforded coccoid forms in spread heated at 100 C.

The CL forms were found to be Gram-positive, nonspore-forming, nonmotile, and strongly catalase-positive. Growth of the rods occurred at 30 and 37 C but not at 45 C. The isolates reduced nitrate, liquefied gelatin, did not produce indole, and in litmus milk caused reduction followed by formation of a soft coagulum and subsequent digestion. Colonies on anaerobic plates of Eugonagar (Baltimore Biological Laboratories) were small, circular, entire-edged, convex, shiny, and white with a pale-brown center. There was no growth on aerobic Eugonagar plates. Acid but no gas was produced from

FIG. 1. Photomicrographs of methylene blue stained preparations of bacteria isolated from (*a*) heat-processed canned fish-spread, (*b*) spice-flour formulation.

TABLE I. Thermal resistance of a typical CL-form nonsporing bacterium isolated from a heat-processed fish product.

	Temperature (*C*)					
	80		90		100	
Time	B[a]	S	B	S	B	S
min						
5	+	+	-	+	-	+
15	+	+	-	+	-	+
30	+	+	-	+	-	+
45	+	+	-	+	-	+
60	+	+	-	+	-	+

[a]B = broth used as heating substrate; S = fish spread used as heating substrate; + = growth.

glucose, sucrose, lactose, galactose and levulose; no acid was produced from maltose, raffinose, xylose, or arabinose.

These results show that the CL rod forms isolated from fish-spreads possess characteristics similar to those of *Corynebacterium acnes* and of the family *Propionibacteriaceae*. The taxonomic position of *C. acnes* and its relationship to the genus *Propionibacterium* have been questioned by Douglas and Gunter (1946) and by Moore and Cato (1963).

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Received for publication March 8, 1966.

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Dry Weight, Ash, and Volume Data for Some Freshwater Planktonic Algae

Numerical records of abundance of phytoplankton in a lake may result in a misrepresentation of the true importance of certain species because of the large differences in size of various planktonic algae. Lund (1964) pointed out that counts of phytoplankton could be made more valuable if data were available on the relationship between cell numbers and dry weight and volume in these species. At present such data are available for only a few freshwater species (Lund, 1961, 1964) and some marine species (Parsons et al., 1961).

Data presented here were collected in conjunction with estimations of standing crops of phytoplankton in Lake Ontario and during an investigation in which excretion rates in various planktonic algae were compared on an ash-free, dry-weight basis (Nalewajko, 1966). All data were obtained using cultures in the exponential phase of growth, to avoid differences in cell composition which may occur in old cultures following nutrient depletion.

Of the 28 species of algae used in this investigation six (no. 3, 4, 9, 15, 20, and 22 in Table I) were obtained from the culture collection at Indiana University and were axenic. *Chlorella pyrenoidosa*, a planktonic strain described by Fogg and Belcher (1961) was also axenic. The remaining 21 species were isolated from Lake Ontario. The Chlorophyceae in this group were axenic. However, attempts to obtain pure cultures of the Bacillariophyceae and *Oscillatoria* sp. were unsuccessful and unialgal cultures were used instead.

Cultures for the determination of dry weight, ash, and cell volume were grown at 20 C and 9150 lux in Chu 10 medium (Chu, 1942) with 10% soil extract in 125-ml conical flasks for 4 days and then transferred to 1000 ml of medium in large flasks for a further period of 7 days. However, in some instances, cultures were inoculated directly into the large flasks and grown for 7–10 days. Addition of soil extract was necessary for growth of some diatoms. The extract was prepared by autoclaving 200 g of garden soil with 500 ml of distilled water and was filtered before use.

For dry weight determinations cells were centrifuged at 1390 *g* for 20 min, washed with distilled water, centrifuged again, and then dried at 105 C to constant weight. Ash content was determined by ignition in a muffle furnace at 550 C.

Cells of small algae were counted in a hemacytometer, larger species were counted in a sedimentation tube or the Lund chamber (Lund, 1959) using an inverted microscope. Clumps of cells or filaments were disrupted by treatment of up to 20 sec duration in the Maxson ultrasonic shaker. This treatment did not cause any breakage of cells unless prolonged for several minutes. A sufficient number of individuals was counted in any determination to give relative standard deviations of 5–10%.

J. Fish. Res. Bd. Canada, **23**(8), 1966.
Printed in Canada.

TABLE I. Dry weight, ash content, and volume data for 28 species of freshwater algae.

Species	Dry weight ($\mu g/10^6$ cells)		Ash-free dry weight ($\mu g/10^6$ cells)		Per cent ash (avg)	Volume (μlitre/10^6 cells)
Chlorophyceae						
1. *Actinastrum hantzschii*	34.1	45.1	30.9	43.3	6.7	0.13
2. *Ankistrodesmus falcatus* var. *spirilliformis*	5.2	5.7	4.7	5.0	10.4	0.03
3. *Asterococcus superbus*	1257	1385	1091	1269	10.8	3.55
4. *Chlamydomonas angulosa*	130.3	164.9	114.1	147.7	11.4	0.41
5. *Chlorella pyrenoidosa*	5.1	6.4	4.5	5.7	11.4	0.02
6. *Chodatella* sp.	129.5	147.2	119.9	132.1	8.9	0.78
7. *Dictyosphaerium ehrenbergianum*	87.5	90.1	79.6	81.1	9.5	0.19
8. *Eudorina elegans*	251.5	292.3	233.0	267.8	7.9	0.32
9. *Gonium sociale*	91.7	106.7	84.5	97.3	8.3	0.53
10. *Micractinium pusillum*	38.4	45.2	35.5	40.4	10.6	0.13
11. *Pediastrum duplex*	195.3	203.6	177.1	181.9	10.0	1.14
12. *Scenedesmus dimorphus*	475.3	621.3	434.5	573.3	8.1	1.13
13. *Scenedesmus quadricauda*	99.7	103.4	91.4	94.4	8.5	0.20
14. *Staurastrum* sp.	4686	4934	4488	4615	5.3	20.50
15. *Stichococcus bacillaris*	13.9	22.9	12.0	18.5	14.8	0.06
16. *Ulothrix* sp.	150.0	194.9	124.3	158.8	19.9	0.39
Bacillariophyceae						
17. *Asterionella formosa*	243.3	291.2	104.8	136.3	55.0	0.65
18. *Fragilaria capucina*	196.7	214.9	98.6	108.9	49.7	0.35
19. *Melosira binderiana*	246.8	281.1	136.7	158.8	44.0	1.38
20. *Navicula pelliculosa*	28.4	37.5	20.5	24.3	31.7	0.09
21. *Nitzschia acicularis*	92.1	93.8	57.3	65.3	33.8	0.28
22. *Nitzschia kutzingiana*	30.7	35.4	17.6	19.9	43.1	0.20
23. *Stephanodiscus astraea*	115.6	122.2	62.8	65.8	45.8	0.31
24. *Stephanodiscus tenuis*	128.3	139.3	89.9	103.2	27.9	0.52
25. *Synedra acus*	271.1	–	157.9	–	27.2	1.31
26. *Synedra ulna*	1953	2086	908	1141	49.5	1.95
27. *Tabellaria floc.* var. *asterionelloides*	383.4	406.6	205.9	209.6	47.3	0.82
Myxophyceae						
28. *Oscillatoria* sp.	262.3	275.3	216.3	211.5	18.6	0.88

Cell volumes were calculated by approximation to geometrical figures if possible, otherwise plasticine models of the cells were made to scale and their volume measured by water displacement.

Most determinations of dry weight and ash were made in duplicate. In a triplicate determination of ash-free dry weight/10^6 cells in *Chlamydomonas angulosa*, relative standard deviation amounted to 14.2%. Experimental error was probably similar in other species.

Dry weight, ash content, and volume data on a cell number basis for 28 species of algae are shown in Table I.

The dry weight and volume/10^6 cells data illustrate the differences in size of various algae. In the species examined here dry weight ranged from

5 $\mu g/10^6$ cells (in *Chlorella pyrenoidosa*) to 4500 μg (in *Nitzschia kutzingiana* and *Synedra ulna*, respectively) in the Bacillariophyceae. Conversion of numerical records of abundance of these species in a lake to dry weight or ash-free dry weight could completely change the order of importance of the species. The importance of diatoms in particular in a standing crop could be reduced by one-third to one-half if ash-free dry weight and not numbers were taken as the basis, since diatoms were found to contain between 28 and 57% ash.

Lund (1964) showed that dry weight to volume ratios fluctuated 5 to 6 fold in the 22 freshwater and marine species which he examined. In the 28 species investigated here the range was somewhat smaller, 170–600 $\mu g/\mu$ litre, with just one very high value of 860 $\mu g/\mu$ litre in *Eudorina elegans* (Fig. 1). It is possible that because of the large variations observed in cell and coenobium size the value for volume of 106 cells of the alga is not very reliable.

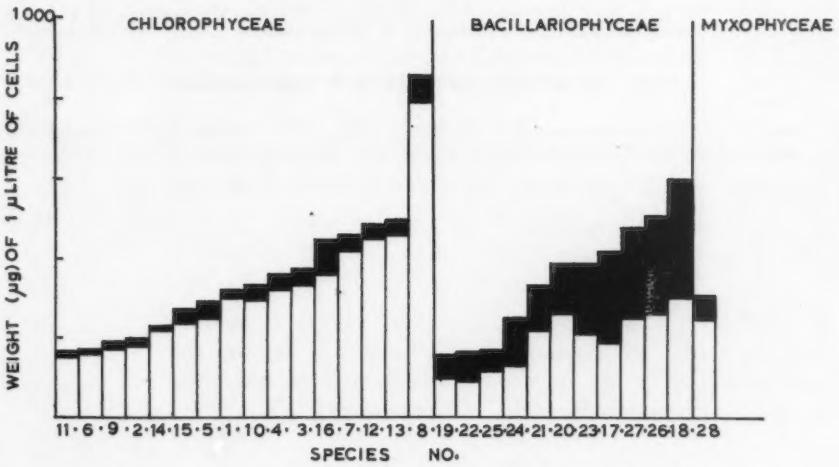

FIG. 1. Dry weight and ash-free dry weight of 1 μlitre of cells in 28 species of algae. Black columns represent the difference between $\frac{\text{dry weight}}{\text{volume}}$ and $\frac{\text{ash free dry weight}}{\text{volume}}$ ratios. For species names corresponding to numbers see Table I.

An analysis of variance for all species (except *Synedra acus*) showed the differences in ratios between species to be significant at the 5% level.

On prolonged growth in culture under the conditions employed here cell size in the diatoms tends to diminish. Although this was to some extent avoided by using freshly isolated cultures, cell size was probably smaller than found under natural conditions in the lake. In particular *Tabellaria flocculosa* var. *asterionelloides* was smaller and the dry weight/10^6 cells lower than the range

given by Lund (1961). In other instances when the same species were investigated here good general agreement with the values given by Lund (1961) was obtained.

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Received for publication February 10, 1966.

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